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Life history and cell structure of Chlorococcum infusionum

HAROLD C. BOLD

(WITH PLATES 32–36 AND FIVE TEXT FIGURES)

Great advances have been made in our knowledge of the unicellular Chlorophyceae since the pure culture methods of Klebs (1896) and Beijerinck (1890) have been followed: the careful work of Chodat, Pringsheim, Smith, and others has shown the stability of algal species during long periods of observation and cultivation. There still remain numerous unicellular species whose occurrence, structure, distinguishing characters, and affinities are obscure. One of the most confused of the genera of Chlorococcales is the genus *Chlorococcum* Fries. The genus is cited by such authorities as West and Fritsch (1927), Printz (1927), Collins (1909), and Rabenhorst (1868), as having been founded by Fries (1825, p. 356), in the appendix of his *Systema Orbis Vegetabilis*. In this work there appears a short diagnosis (without mention of species) as follows:

> A. Chlorococcum—Granula libera, minima, colorata (viridia l. rubra) absque gelatina. *Fries S. M.* 1820.

The last phrase is a citation of an earlier work by the same author, the *Systema Mycologicum*, volume 1, in which the name *Chlorococcum* is published for the first time (p. xxii), without diagnosis but based on the typifying species *Tremella botryoides* Schreber (*Nostoc botryoides* Agardh). This reference to the more effective publication in the *Systema Mycologicum* has evidently been overlooked by the majority of systematists, for the date of founding of the genus is usually given as 1825; Brunnthaler (1915) alone has recognized its earlier publication, citing the date as 1820.[1] An excellent summary of the taxonomic history of the genus is given by Puymaly (1924). It is important to note that the early descriptions of the genus *Chlorococcum* by Fries (1821, 1825) and Greville (1827), are not adequate to delimit this genus from other spherical protococcoid forms, so that we are compelled to base our present conception of the genus on the more detailed accounts of Meneghini (1842), Nägeli (1849), Rabenhorst (1868), Famintzin (1871), Artari (1892), Bristol (1920), and Puymaly (1924).

The present paper presents observations on a unicellular green alga which I have identified as *Chlorococcum infusionum* (Schrank) Meneghini,

[1] The first volume of the *Systema Mycologicum* was not published until 1821, although the preface is dated 16 Nov. 1820.

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based on pure culture methods and cytological preparations. As I have noted below, the organism appeared first in an old culture of undetermined origin. I have obtained an organism from Vermont soil cultures, similar to the original organism in apparently every respect, except for a slight deviation in size. I have also observed a similar form which appeared in uncorked bottles of weak salt solutions, which were stored in the greenhouse of the University of Vermont; this organism also was similar to the original alga.

The genus *Chlorococcum*, and particularly the species *C. infusionum*, has rarely been reported in America. I have examined specimens of the *Chlorococcum* species in the Collins Herbarium at the New York Botanical Garden, and so far as I can ascertain from the dried material, the organism I have studied is essentially similar to two specimens identified as *C. infusionum*—the one by N. L. Gardner, collected in 1906 in a roadside trough in Berkeley, California, and the other a specimen of F. S. Collins, collected on grasses in a pool at Nahant, Massachusetts, in 1903. In cell size these specimens are in agreement with the material I have worked with, and their aggregation of angular cells into a loose coenobium-like mass seems to confirm the identification I have made. The infrequency with which this form has been reported may possibly be correlated with the great difficulty in identifying it with certainty. If one goes back to the original description by Schrank (1794) of his

Lepra infusionum viridis, glomerulata, in pelliculam continuam concrescens,

or even to his later account (1811) of *Lepraria infusionum*, which is usually cited as the first description of this species, one finds little that is satisfactory to a modern algologist. Nevertheless it is probably best to maintain this historic specific name as it has come down to us through the amplified description of Meneghini (1842) and later students.

The work was begun at Columbia University in 1928 at the suggestion of Professor C. C. Curtis; I take this opportunity of expressing gratitude to him and also to Professor R. A. Harper for valuable criticism and suggestions; also to Professors B. F. Lutman and A. Gershoy of the University of Vermont for suggestions and aid in interpreting some of the cytological preparations.

MATERIAL AND METHODS

The original source of the alga is unknown; it appeared first in an old culture which had remained in the botanical laboratory of Columbia University for many years. It was growing in water filled with organic material, amid an abundance of Myxophyceae, bacteria, and fungi. Dilutions were made and cultures started in Poland Spring water, Knop's

and Detmer's solutions, and other solutions of inorganic salts recommended for growing algae. The cultures were grown in a north window, at a more or less constant temperature of 20° C. After several weeks the *Chlorococcum* had increased greatly, and platings were made on a 1 per cent agar medium made with 0.2 per cent Knop's solution. Within three weeks, growth was sufficient to be perceptible macroscopically, the algal colonies appearing among numerous bacteria. One of the methods given by Schramm (1914), was followed in obtaining pure cultures. Plates showing good growth were allowed to dry slightly for a week. At the end of that time, small colonies of the alga were transferred to vials of sterile distilled water. Zoospores were immediately liberated from the parent cells and swam to the surface of the liquid. These were removed with a platinum loop and spread in a drop of nutrient solution over the surface of sterile agar, in a petri dish. Pure cultures were obtained from these zoospore platings. This method is probably equally adaptable to all algal forms with motile spores. These pure cultures were transferred repeatedly both in liquid and solid media, in order to obtain most natural conditions; agar cultures were prevented from drying by means of a silver foil cap sealed with vaseline. For direct observation, hanging drop cultures were employed, and in favorable cases these could be kept in good condition for relatively long periods.

Material was fixed from cultures growing rapidly both in nutrient liquids and on nutrient agar. For the material from liquid cultures, the method used by Lutman (1910) for imbedding *Closterium* proved very valuable.

In fixing material from agar cultures, small rectangular blocks of the medium with the organism were cut out and dropped into the fixing solution; the organisms adhered to the agar throughout the following processes. Fixations were made at intervals in the daytime, and two series were conducted at half hour intervals, from nine in the evening until four-thirty the following morning.

Merkel's fluid, acetic corrosive sublimate in 70 per cent alcohol (used at 85° C.), Allen's B-15 solution, Flemming's medium solution, Flemming's weaker solution, and Flemming's weaker solution diluted with an equal quantity of water, and the chrom-acetic fixative recommended for algae by Chamberlain, were the fixing solutions used. Numerous trials showed that the Flemming's solutions, Allen's B-15 solution, and acetic corrosive sublimate gave excellent fixation without visible distortion.

A few preparations were made by the smear method, but for critical work, the material was dehydrated, cleared, and imbedded in paraffin, sectioned at from one to five microns. Sections were stained both in Flem-

ming's triple stain and in iron haematoxylin, counterstained in some cases with alcoholic eosin.

Some material from each fixation was stained in both the triple stain and the haematoxylin, since in certain stages (cleavage and in young vegetative cells), the distinction between the nucleus and pyrenoid is made only with great difficulty with the haematoxylin, but is more readily demonstrated with the triple stain.

CULTURAL CHARACTERS

On solid media, growth is always confined to the surface of the agar film, and occasionally occurs between the surface of the agar and the wall of the vessel, when there is sufficient space to permit the entrance of air (figs. 1, 2, 3). The organism forms a more or less circular colony about the point of inoculation (figs. 2, 4). As the age of the culture increases, the color of the plant mass changes from a pale yellow green to a deep olive green. This is due to the increased number of green cells concentrated at a given point, and also to the numerous zoosporangia with overlapping zoospores. Mounts made from old agar cultures show that almost every cell, regardless of size, has undergone zoospore formation (fig. 7). The color is never any color but green, even in cultures retained for as long as two years.

Multiplication of the organism takes place in agar cultures, usually by means of zoospores as long as the moisture is sufficient to permit their liberation. Mounts made from drying cultures show most of the mother cells filled with aplanospores which are similar to zoospores, except that they develop cell walls soon after they are formed and omit the motile stage (fig. 22).

Disc-shaped colonies are formed on the surface of the medium by the swarming of zoospores in all directions from the point of innoculation. For example: four Petri dishes with a thin film of solidified nutrient agar (0.2 per cent Knop's) were innoculated once each with zoosporangia from an old agar culture, on February 20, 1929. The zoosporangia in the surface film of liquid on the agar immediately burst, liberating many zoospores. These swam about in the liquid surface film, and spread to considerable distances from the original point of innoculation. Thirty hours after innoculation the majority had become quiescent and collected in small groups here and there on the surface of the agar. By February 24, these quiescent zoospores increased in size to almost the size of their parents (as far as could be determined under a 16 mm. objective), and by February 25 had themselves formed zoospores which were liberated in the morning.

Meanwhile the thin agar films had dried considerably and the surface film of water was no longer continuous over the entire surface of the agar, but confined to small droplets which collected about groups of what were the original zoospores. Therefore this second generation of swarmers was more limited as to the area over which it could become dispersed. These zoospores became quiescent within approximately twenty-four hours and began their development. By March 2, these in turn had enlarged and undergone cleavage, so that a third generation of zoospores was liberated. These last zoospores were still further limited as to the possible radius of motility, due to continued drying. Observations ceased after this point. Growth by this time was sufficient to be perceptible macroscopically. Increase in numbers in moist cultures is always effected by this method. Examinations of the disc-shaped colonies always show a predominance of old cells or zoosporangia in the center, and proceeding outward towards the margin of the colony a progressively greater predominance of younger cells.

After the culture has dried, multiplication is effected by aplanospore formation, the large mother cells undergoing cleavage as if in preparation for zoospore formation. The daughter protoplasts, however, are retained within the mother cell membrane, where they develop walls and continue their growth into mature vegetative cells; the mother cell membrane usually disappears, owing to the pressure caused by their growth. This process is in turn repeated in the daughter cells, so that in dry cultures there may appear small mounds of cells above the surface of the substratum, which are composed of extensive cell complexes. If these cultures are moistened, zoospore formation is again initiated; this can be shown by cutting out a small block of agar with aplanosporangia, and mounting in water on a slide. The aplanospores develop cilia, are liberated from their walls and swarm, in the same way as zoospores. Many empty mother walls may be seen containing the empty walls of the aplanospores.

In liquid cultures, the alga forms a thin film over the surface of the liquid, and a ring on the sides of the dish, which may extend as far as a centimeter above the water level, in the surface film of moisture on the glass. This is an expression of either the pronounced positive aerotactic or thigmotactic response of the zoospores, when they are set free. Multiplication in liquid cultures of low nutrient content is in general by means of zoospores. These are set free in undisturbed cultures in the morning, as a result of the previous evening's cleavage; examination of a drop of liquid from such cultures early in the morning usually reveals numerous swarmers. In solutions of higher concentration multiplication is by means of aplanospores.

CELL STRUCTURE

Cell size and form. The cells when isolated are globose to spherical in form (fig. 11). Isolated cells are most often found in the water at the bottom of liquid cultures. They are probably cells which have sunken from the surface film and come to rest on the bottom of the dish. It is of interest to note that such cells are usually filled with starch reserve, and it is probable that the change in specific gravity may be correlated with loss of buoyancy. Cells in the surface film present quite a different form from those at the bottom of the culture. They are always associated to form a flat expanse of polyhedral cells (figs. 5, 6, 7, 8, 9, 10). In young cultures where this surface layer is one cell thick the cells appear hexagonal in optical section, the sides of the hexagons forming 120° angles (figs. 8–10). The polar cell surfaces are curved. This is a direct response to the crowded conditions in which the cells grow. Cells separated from the mass readily assume the spherical form. Figures 7, 9, 10 show aggregations of cells from a surface film. The surfaces of cells which are in contact with other cells are flattened, while the free cell surfaces remain rounded. Each cell in this aggregate could become spherical if separated entirely from the mass. In older cultures where the surface layer of the culture is composed of several superimposed cell expanses the tangential surfaces of the cells are flattened as they are in a single layer, but the polar walls which are in contact with other cells are also flattened in this case. As Famintzin (1871) notes, these expanses of angular cells are precisely similar to what Kützing (1843, 1845, 1846) described in his *Limnodictyon Roemerianum*, so that there may be some justification for considering the latter synonymous with or a variety (Brunnthaler, 1915) of *Chlorococcum infusionum*.

Cell size varies from 9 to 40 microns in diameter; cleaving cells most often measure between 18 and 30 microns; larger cells are less numerous. In measuring angular cells, the diameter was considered to be the distance between poles. Immature cells, i.e., developing zoospores, range from 2.8 microns upwards.

The cell wall. The protoplast is bounded externally by two layers (fig. 12): the innermost layer is composed of cellulose and the outer is of mucilaginous nature. The cellulose wall is thin in younger cells, but thickens slightly as the cell grows older. Adjacent to this on the outer side is a layer of hyaline mucilaginous material, which is itself clearly delimited from the surrounding medium (fig. 12). In cells treated with iodine and sulphuric acid, the inner membrane swells slightly and stains deep purple-blue. The outer layer is not altered except for the fact that its lamellate structure, often seen with some difficulty in the living condition, becomes more clearly visible. It is of interest to note that the material forming the

so-called 'striations' between the lamellae also stains various shades of blue; those nearer the inner membrane stain deeper and become progressively lighter blue, proceeding from the innermost lamella outward. The lamellae themselves remain unstained. Figure 12 is a semi-diagramatic representation of a cell immersed in iodine and sulphuric acid. A slight shrinkage of the protoplast has occurred, presumably as a result of the acid. This cell has unusually thick bounding membranes, and consequently illustrates the structure very clearly. Occasionally the outermost striations appear more delicate and are not so sharply continuous as in the present case.

Similar reactions occur in cells treated with chlor-zinc-iodide. From these results I have concluded that the inner membrane, adjacent to the protoplast, is composed of cellulose. The differential staining in the outer layer, of the lamellae and the material between them, is of interest. Beijerinck was of the opinion that the slime layer of some acetic acid bacteria showed in tests a decided affinity with cellulose. The staining reaction of the outer layer of the cells of *Chlocococcum infusionum* apparently substantiates this view. It is probable that the mucilaginous material is a product of hydrolysis of cellulose, and that the material between adjacent lamellae represents an 'interphase' in which hydrolysis has not progressed as far. There is further support for this view in the behavior of the cellulose inner wall during cleavage, at which time the cellulose wall of the cleaving cell becomes transformed into a gelatinous substance to permit the escape of the zoospores.

In fixed, sectioned, and stained material, the wall appears as a homogeneous zone outside of the chloroplast, and in the triple stain stains lightly with Orange G. In general, as noted above, the bounding membranes of young cells are thinner (figs. 13, 14) and they increase in thickness as the age of the cell increases (figs. 5–8). In the vegetative cells, developing after the zoospores become quiescent, the cellulose wall appears as an extremely delicate, orange-staining film, most clearly seen where the protoplast shrinks slightly from the wall.

The chromatophore. The chromatophore, in all accounts of *Chlorococcum*, is described as parietal and as either completely or partially covering the inner surface of the plasma membrane. Nägeli (1849) and Famintzin (1871) observed cells in which the chlorophyl was continuous, and other cells in which there was an opening, or colorless area where chlorophyl was absent. I find a similar variation; apparently the presence or absence of this opening is not a fixed character. In swarming zoospores the chlorophyl is confined to a plate or band-shaped zone, which may more or less completely cover the inner surface of the plasma membrane (figs. 13,

36–38). As the zoospore develops into a mature cell, the area where chlorophyl is present gradually increases until the entire periphery of the cell contains chlorophyl, or a small colorless area may remain. Figures 13–18 show a series of stages in the development of a zoospore. The chlorophyl appears to increase in amount and diffuse superficially through the cytoplasm as the cell grows, until only a small area of colorless cytoplasm is left (fig. 18). This is continuous with cytoplasm which fills the interior of the cell. This is clearly shown in preparations fixed in corrosive sublimate, which preserves the chromatophore plainly. Figure 23 shows such a cell, which is not quite mature and in which the opening of the chromatophore is still quite large. This cell corresponds approximately in its stage of development to the living cell shown in figure 16. The colorless cytoplasm is often very watery and may contain several small vacuoles and many oil droplets (figs. 11, 27).

The structure of the chromatophore is most clearly demonstrated in cells which are packed with so called 'stroma starch' grains. The starch occurs in the form of minute ellipsoidal or wedge-shaped grains, as shown in figures 23, 26, and 48; these grains are always imbedded in the material of the plastid, and never found in the colorless cytoplasm. In triple stained preparations they stain with avidity with gentian violet, giving the entire chromatophore a purple tinge, so as to delimit it sharply from the colorless cytoplasm, which stains light yellow.

Often the chromatophore is filled with very numerous minute oil droplets, which are readily blackened with osmic acid, and stain sharply with Sudan III. Bristol (1920) and others note that cells of *Chlorococcum* develop droplets of red oil which give the cells a dark brown appearance. I cannot identify these small oil droplets present in the chromatophore with those reported above, since I have never found them to be colored. In fixed and stained preparations the oil droplets are removed by the alcohols and clearing agents, so that the chromatophore often appears alveolar.

The pyrenoid: its relation to starch formation. The pyrenoid is a characteristic structure present in algal cells, but as to its nature and functions, considerable divergence of opinion exists. Schmitz (1884) showed that the pyrenoid is a spherical, proteinaceous body, which lies imbedded in the substance of the chromatophore, just as the nucleole is imbedded in the nucleus. He associated starch formation with the pyrenoid, but held the view that while the starch is formed from that body, it is formed in the surrounding cytoplasm from the material of the pyrenoid, but not in the pyrenoid itself. Similarly, Meyer (1883), describing the pyrenoid as sometimes angular, is inclined to the view that it is merely a proteinaceous deposit. Schimper (1881), investigating simultaneously with Schmitz and

Meyer, came to the conclusion that the pyrenoid is of the nature of a protein crystal, and agreed with Schmitz as to its relation to starch formation. The recent voluminous review of the literature of this subject by Czurda (1928) renders it undesirable here to do more than emphasize the particular papers of most interest in connection with the present study.

Chmilewskij (1896), from his study of the pyrenoids of *Zygnema* and *Spirogyra*, concludes that they are definitely organized cell structures. He finds that they always divide at cell division, but he is not specific as to how they are associated with starch formation. Dill (1895) finds a similar division of the pyrenoid at cytokinesis in *Pyramimonas*. A more definite account of the relation of the pyrenoid to starch formation in *Hydrodictyon* is given by Timberlake (1901), who is able to show, in cytological preparations, that the pyrenoid consists of a central protein mass, from which tangential segments are apparently successively cut off. These pieces, pushed out into the cytoplasm by the continued segmentation of the original protein mass, are progressively changed to starch. The staining relations bring out this sequence, the central proteinaceous mass taking the safranin brilliantly, and the segments proceeding centrifugally from the center staining in progressive stages of red, gray, purple, and finally blue. These segments, cleft from the original pyrenoid body, develop into starch grains.

McAllister (1914) describes the compound pyrenoid of *Anthoceros* as consisting of 'from 25 to 300 closely aggregated disc or spindle-shaped bodies which I have called pyrenoid bodies.' He finds that the outer 'pyrenoid bodies' of this compound structure become directly transformed into starch grains. He describes the differential staining of pyrenoid and starch as similar to that in *Hydrodictyon*.

Smith (1914) finds in *Scenedesmus* that the pyrenoid is either angular or spherical and that under certain conditions it may be surrounded by a peripheral layer of starch segments which have been cleft off from the pyreno-crystal. He further finds that during autocolony formation, the original pyrenoid is transported to one of the four daughter cells and pyrenoids arise *de novo* in the other three. In *Tetradesmus* Smith (1913) finds a circular layer of starch segments surrounding the pyrenoid. Here also he describes a similar origin of pyrenoids *de novo*, in the cells of the auto-colony. In *Characium* (1916a) he is unable to show the origin of starch from the pyrenoid, but finds numerous starch grains present just within the plasma membrane. He assumes, on the basis of Timberlake's work, that these are the so-called 'stroma starch grains,' which have migrated to the periphery because of their lightness. He reports the disappearance of the pyrenoid during cleavage, and the formation of a pyrenoid *de novo* in

the daughter protoplasts. In *Pediastrum* (Smith, 1916b), the pyrenoid is surrounded by a layer of thin, curved starch plates. He finds, as did Lutman (1910) in *Closterium*, that the pyrenoid body during starch formation is not always homogenous but stains unevenly. In *Pediastrum* also the pyrenoid disappears during the earlier stages of cleavage and each daughter cell develops one *de novo*.

Miss Bourquin (1917) who re-investigated the pyrenoid and plastid of *Zygnema*, reports that starch is formed, not from the pyrenoid, but arises in the form of small grains at the periphery of the chloroplast. Her results are diametrically opposed to those of Chmilewskij, in respect to the same material.

Miss Carter (1926) has given an account of the structure and behavior of the pyrenoid during cleavage in *Ulva* and *Monostroma*, but is concerned primarily with the nuclear divisions which precede cleavage, and has not studied starch formation. She finds that the pyrenoid behaves in two distinct ways prior to cleavage. It may fragment into small pieces, each of which is capable of reorganizing into a new pyrenoid in the daughter cells, or it may dissolve as shown by its loss of staining capacity, and what remains of it at the end of cleavage may be transferred to one of the daughter protoplasts. Pyrenoids arise *de novo* in the others.

Recently Kater (1929) has reported interesting observations on the pyrenoid of *Chlamydomonas nasuta*. He reports and emphasizes the fact that the pyrenoid does not lie imbedded in the chloroplast, but lies in the colorless cytoplasm with the nucleus. The pyrenoid core he has demonstrated to be reticular and not homogeneous as it has been generally described. Surrounding the pyrenoid is a hyaline area of variable extent. He finds that 'this part contains the starch, which, supposedly, is formed by the pyrenoid.' This hyaline zone is traversed by radial strands. During nuclear and cell division the pyrenoid core becomes transformed into a cytoplasmic alveolus, as does each of the starch segments surrounding it. After cytokinesis a pyrenoid, *with a starch ring*, arises *de novo* in each of the daughter cells, by the condensation of material in a cytoplasmic alveolus.

In *Chlorococcum infusionum* each cell contains a pyrenoid, which is the most conspicuous feature both in living cells and stained preparations. It stains densely with the safranin of the triple stain and with haematoxylin (figs. 23–26). Often a cell may contain two pyrenoids, one of which is generally smaller than the other (fig. 30). The presence of two pyrenoids may result if a zoospore receives two pyrenoid fragments during cleavage. At certain times the pyrenoid assumes an elongated, constricted or dumb-bell shaped form (fig. 55) similar to the pyrenoids of *Characium*, and the pyrenoid often appears to have been divided by constriction (fig. 56). It is possi-

ble, as Smith suggests, that these figures may represent a division of the pyrenoid similar to the division Chmilewskij (1896) has described for *Zygnema*, but I have been unable to trace the further development of these elongated and divided pyrenoids.

The pyrenoid body of *Hydrodictyon*, according to Timberlake, assumes a spherical shape only during periods of relative inactivity. In pyrenoids from which starch is being rapidly formed, the central mass is always of an angular or irregular shape because of its segmentation. In the cells of *Chlorococcum infusionum*, the pyrenoid is almost never completely spherical if the cultures have been standing in the light, that is, if starch formation is taking place. It consists either of a more or less irregularly lobed structure (figs. 18, 24) or seems to be compound (figs. 43, 45, 46, 50, 54) and made up of separate pyrenoid bodies or fragments of one pyrenoid body (figs. 50, 51).

Surrounding the pyreno-core is a hyaline zone which has been reported for every other alga cytologically investigated (figs. 39 to 59). This zone apparently contains a watery substance without affinity for any stain. Occasionally it appears to be faintly stained with the Orange G, but I cannot say definitely whether this appearance may not be due to a reflection of the stain of the general cytoplasm. This observation is of interest in view of Denniston's (1907) observations on the structure of starch grains, in which he notes that there is a 'specially differentiated orange staining layer' present between the starch and the plastid, both in growing and corroded grains. He is inclined to the view that this orange layer is a transition zone, chemically different from the starch. As I shall point out later, there is apparently evidence that the hyaline or faintly orange staining zone between the pyrenoid and starch ring in cells of *Chlorococcum* is a transition zone, in which the final stages of hydrolysis of the protein fragments of the pyrenoid body take place, and in which a more or less soluble carbohydrate is formed, which is ultimately deposited in the surrounding cytoplasm in the form of starch.

The hyaline zone is usually bounded on the periphery in all cells from well lighted cultures by a thinner or thicker layer of starch (figs. 16, 19, 23–30). This sheath of starch always stains blue with the gentian violet. In some cases the starch sheath is very delicate (figs. 43, 45, 52), and might be easily overlooked in superficial examination. In other cases it may reach three fourths of a micron in thickness (figs. 39, 40, 51, 54). I have never found more than one ring of starch around the pyrenoid.

The starch sheath appears to be very finely granular and is composed either of a continuous structure like a hollow sphere, or it may be composed of several segments of a sphere, of variable thickness. This is best seen in optical section.

No one since Timberlake has been able to show definitely that the starch segments have a genetical relationship to the proteinaceous pyrenoid crystal. Lutman (1910) describes the pyrenoid of *Closterium* as cracked along planes which would correspond to the sectors of starch grains, but cannot show definitely that these pieces of pyrenoid which are separated from the main body of the pyrenoid by a fissure, become directly of their own substance transformed into starch grains.

In *Chlorococcum* I have observed so far no direct transformation of a pyrenoid segment into a starch grain. I find numerous cases (figs. 23, 24, 26, 40, 43, 46, 49, 53) where the pyrenoid is cleft either into two or numerous parts, but I have been unable to follow their migration from the pyrenoid to the cytoplasm and their direct transformation into starch as reported in the case of *Hydrodictyon*. I have observed that usually these segments which are cleft from the pyrenoid may withdraw slightly from the main body, whereupon they decrease in size and their staining reaction changes (figs. 39, 40, 44, 46). Instead of staining a brilliant red, they take a dull reddish-purple stain. It is my opinion that these segments dissolve and are present in the hyaline zone in soluble or slightly soluble form, which explains their incapacity to be heavily stained. In my opinion in this hyaline zone there takes place the transformation of the proteinaceous pyrenoidal material into a soluble carbohydrate, which is finally deposited in the surrounding cytoplasm to form the starch sheath.

Unfortunately, the morphological changes involved in starch formation have not been directly corroborated by a chemical explanation. Timberlake (1901) was of the opinion that starch formation involved the hydrolysis of a protein:

> The fact that, as seems to be well established by various observers, the pyrenoid is of a proteid nature, and that a portion of it—at least in *Hydrodictyon*— is converted into starch, suggests that the process involves the breaking down of a proteid into a carbohydrate.

As to the actual steps in chemical transformation we know very little. It is possible to conceive of the protein molecule as extremely complex, having many 'side chains,' which may be added to and disassociated from the protein molecule. We can conceive of the protein molecule as a 'carrier' of carbohydrate side chains which may at times be cut off. (This conception of the protein molecule as a 'carrier' is well illustrated in the case of haemoglobin in the blood which is carried by the protein molecule.) It may well be that in the present instance the carbohydrate 'side chain' is 'cut off' and diffuses out evenly in all directions away from the main aggregation of protein molecules (the pyrenoid body).

The cytological evidence in this alga makes the 'side chain' hypothesis

seem to be very plausible. The conception of the protein molecule as a 'carrier' is visibly expressed here and the pyrenoid (the particular protein molecule under discussion) does not disappear nor in fact ever decrease materially in size.

Starch formation in *Chlorococcum infusionum*, and perhaps in all the other forms investigated, where there is no obvious progressive transformation of the pyrenoid material into a carbohydrate, seems possibly to suggest that carbohydrate 'side chains' are lost by the protein molecules of the pyrenoid body. These carbohydrate 'side chains' may be present in the hyaline zone in a soluble form and appear finally in the protoplasm surrounding this zone as the carbohydrate, starch.

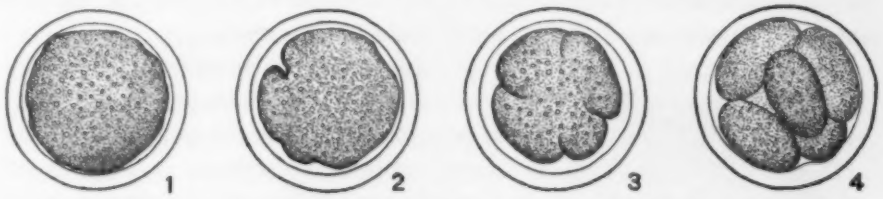
The pyrenoid is plainly dependent on light for starch formation. Cultures of the alga were left in darkness for periods up to five days; fixations were made after various periods of growth in darkness. Preparations show all stages in the disappearance of the central body (figs. 57–59). It loses its red-staining capacity and at first stains a little darker than the surrounding cytoplasm (figs. 57, 58), and finally so pale as to be hardly visible. In several cases the starch ring remained as a narrow zone which stained brilliantly after the pyrenoid disappeared, but generally the starch was completely used during the period of darkness. Lutman (1910) observed a similar phenomenon in darkened cultures of *Closterium*.

In *Hydrodictyon*, Timberlake demonstrated clearly, in my opinion, that all starch present in the protoplasm has its origin in the pyrenoid. Smith (1916a) shows that the starch in *Characium* migrates centrifugally from the pyrenoid to the plasma membrane. I have found, usually from cultures in which reproduction was almost at a standstill, numerous cells of *Chlorococcum infusionum* in which the protoplast was filled with grains of so called 'stroma starch' of Klebs, as in figures 23, 26, 48. The relation of this 'stroma starch' to the pyrenoid is not evident except in carefully stained preparations. I have noted above that the pyrenoidal starch ring is not always continuous, but often separated into several segments. In cells with 'stroma starch,' such as those shown in figure 48, the starch ring is usually not continuous but cleft into two or more segments, whose tangential portions show fissures which result in the separation of small starch masses; in figure 54 several 'stroma starch' grains are separating off from the pyrenoidal starch ring. These apparently migrate centrifugally, as Smith has shown in *Characium*. Their origin in the pyrenoid starch ring is further established by their shape, which is identical in grains still attached to the ring and those which have migrated out. My observations on *Chlorococcum infusionum* substantiate the conclusion of Timberlake and Smith that all starch in algal cells with pyrenoids originates from the pyrenoid.

REPRODUCTION

Asexual multiplication in *Chlorococcum*, as Nägeli (1849), Famintzin (1871), Artari (1892), and Bristol (1920) have shown, is effected in two distinct ways, depending largely on environmental conditions. Nägeli observed the formation and liberation of non-motile gonidia. Puymaly (1924) attributes Nägeli's failure to observe zoospores in *Chlorococcum* to the heterogeneous mixture of protococcoid algae in his culture. Famintzin describes and figures zoospore formation, and the production and development of 'eine grosse Menge unbeweglicher Kügeln,' the former produced in weaker solutions, and the latter in nutrient solutions of higher concentration: both types are formed by a simultaneous division of the mother cell. He describes the zoospores as being elongated and after a period of motility as coming to rest and developing until they reach the size of the mother cell, whereupon they themselves undergo cleavage. The non-motile reproductive cells, according to Famintzin, are formed in a similar way; they may begin their development while still enclosed in the mother cell wall, or may first be set free. Even after being set free they often hang together in clumps and by further internal cleavage, may build up cell aggregations of considerable complexity. Famintzin's observations were made on *Chlorococcum infusionum*, and no sexual reproduction is reported. Artari's later contribution to the knowledge of *Chlorococcum* is also based on observations of *C. infusionum*, in which he describes reproduction by zoospores, and by non-motile cells which are similar to those described by Famintzin. There is however, one point of disagreement: Artari emphasizes the point that the reproductive cells arise by successive divisions in a mother protoplast into two, four, eight or more cells; Famintzin, on the other hand, describes the process as one of simultaneous cleavage of the mother protoplast. Artari adds details as to the structure of the zoospores, namely the presence of a single nucleus and pyrenoid, 2 cilia, an eye spot, and 1 or 2 (?) contractile vacuoles; the zoospores are set free by the bursting of the mother cell membrane which is clearly composed of two layers. He also notes that older cells are always multinucleate, and finally that reproduction is never by cell division but always by endogenous divisions to form either zoospores or gonidia. A more modern cytological account of *Chlorococcum* is presented by Miss Bristol (1920) for *C. humicolum*, which is, according to Puymaly and others, synonymous with the *Cystococcus humicola* of Nägeli (1849) referred to above. She records for this species also, the production of biciliate zoospores and non-motile gonidia, noting that the latter are really zoospores which omit a motile stage. Zoospores are formed by successive bi-partition of the mother cell contents into eight, sixteen, or an indefinite number of portions. The aplanospores or non-motile repro-

ductive bodies, on the contrary, according to Miss Bristol, arise as a result of a preliminary nuclear multiplication (by constriction), following which each nucleus becomes the center of a mass of cytoplasm. The delimited individual aplanospores become angular by compression, and are finally liberated by the rupture of the mother cell membrane, and may remain associated in jelly in somewhat of a palmelloid condition. Her account does not make clear why aplanospores, which differ from zoospores only in the omission of a motile period, should differ so much in the method of their formation from the latter motile bodies. Conjugation of motile cells and formation of zygospores are described and figured. Puymaly (1924) reports three cases of conjugation and zygospore formation, also for *Chlorococcum humicolum*, but gives no details of zoospore formation.



Figs. 1–4. The same vegetative cell drawn at intervals during cleavage to form zoospores. In fig. 1 the protoplast has withdrawn slightly from the wall and has an irregular boundary; 7:55 p.m. In fig. 2 the first indication of a surface furrow is shown, with furrowing just beginning at other points at the surface; 8:40 p.m. Fig. 3, drawn at 9:35 p.m.; the furrows are meeting, isolating portions of the chromatophore. Fig. 4, Cleavage complete, six zoospores visible in the upper focus; 10:40 p.m.

I have been able to confirm in general the descriptions of zoospore formation and production of non-motile reproductive cells referred to above, in my study of living and fixed and stained cells of *C. infusionum;* in several rather important details my observations are at variance with those of Artari for the same species, and those of Miss Bristol for *C. humicolum*.

Multiplication by zoospores. The predominant method of multiplication in *C. infusionum* is by means of zoospores, which arise through the endogenous division of the contents of a vegetative cell. In living cells the first indication of zoospore formation is a slight contraction of the protoplast from the cellulose membrane (text fig. 1), followed by a gelatinization of the cellulose wall. In undisturbed cultures cleavage generally occurs between the hours of seven in the evening and three in the morning. Cultures examined during this period show all stages in the process, from the formation of the inner gelatinous vesicle to the the final products of division. Text figures 1–4 are camera lucida drawings of the same cell at critical

stages in the process. The pyrenoid or pyrenoids disappear before the initiation of cleavage. It is very difficult to follow the exact fate of this body but the cytological evidence seems to show that it fragments into a number of pieces. There appear throughout the surface of the chromatophore narrow areas (text figs. 2, 5) which appear clear and watery, gradually extending both internally and peripherally isolating small islands of the cytoplasm, each with a portion of the chromatophore. These clear spaces appear distinctly as invaginations near the surface, but toward the interior become narrower so as to appear as rather delicate lines (fig. 31). These small islands of cytoplasm are at first angular, but later develop rounded margins (text figs. 3, 4) and finally become elongated and oval (text fig. 4). They seem to contract somewhat and become separated from each other by greater distances. They remain in this condition in undisturbed cultures until early morning, when they are liberated as zoospores.

Fig. 5. A larger cell than that shown in figures 1–4 undergoing cleavage. Note the broad surface furrow somewhat '**H**' shaped. This zoosporangium produced approximately 38 zoospores.

At the time of liberation and immediately before, each zoospore is equipped with a small pyrenoid at the lower end of the chromatophore, a lens-shaped stigma imbedded peripherally, near the anterior end of the chromatophore, two cilia which originate at the anterior end, and a single minute nucleus (figs. 13, 20, 21, 36, 38).

Shortly before their escape, these small protoplasts show slight signs of motility. At first the motion is very feeble and consists merely of a gliding movement of the cells, but later the cilia begin to beat rapidly and the interior of the zoosporangium is transformed into a cluster of motile zoospores. During this phase of their movement the zoospores are seen to lie in a sac of jelly, of an almost liquid consistency, which is bounded externally by the gelatinized cellulose wall. This gelatinous vesicle is stretched peripherally as the zoospores struggle to free themselves; finally sufficient pressure is set up to burst the outer gelatinous membrane of the cell at one point (fig. 21). The inner gelatinous sac with the zoospores is dislodged into the water; here they become still more active as the gelatine dissolves, and finally are set free into the surrounding medium. It often happens that the outer membrane does not open sufficiently to permit the extrusion of the gelatinous vesicle and in this case the zoospores often escape singly or in small

groups, and occasionally one or two may be left behind, where they may become quiescent and complete their development.

The number of zoospores produced in a zoosporangium and especially their size is exceedingly variable, being largely dependent on the size of the mother cell; the size and number produced are correlated with its size. In cultures where zoospore formation is proceeding rapidly, even the smaller cells undergo cleavage (figs. 7, 19), and very small zoospores, 2.0–3.5 microns long, are produced. These swim about like the larger individuals and are able to complete their development into mature cells. From two to over forty zoospores may arise from a single sporangium, depending on its size. In cells 18–20 microns in diameter, 12 to 24 spores is the normal range. In smaller cells a correspondingly smaller number is normally produced. Both Artari (1892) and Famintzin (1871) report the number of zoospores as always a multiple of two but I have been unable to confirm this.

It is of interest to compare zoospore formation in living cells with material fixed, sectioned, and stained. For this purpose material was fixed from cultures both in liquid and on agar, as noted above. The first indication of cleavage in fixed material is the multinucleate condition (fig. 27). Artari finds that as the zoospore develops, the nucleus divides so that in mature vegetative cells there are always many nuclei, a condition similar to that existing in *Hydrodictyon*. I find that in every case the multinucleate condition is a direct forerunner of cleavage. In the same culture vegetative cells of the same size may be either uni- or multinucleate, depending on how soon cleavage is to follow. Miss Bristol (1920) accepts West's (1916) statement that the mature cells of *Chlorococcum* are coenocytic, especially those of *C. humicolum*. In preparations made from material fixed from cultures where many cells were cleaving, I have found many nuclei in the spireme condition (fig. 25) but no later division stages clear enough to merit discussion. The nuclei are exceedingly minute after the divisions preceding cleavage, having a diameter of 0.75–1.0 micron. They assume a peripheral position in the cell (fig. 27).

The pyrenoid at this stage begins to disintegrate by fragmentation (fig. 28). The central proteinaceous mass is cleft into numerous spindle-shaped segments which are distributed in the cytoplasm (figs. 29–31). At about this time, the cellulose wall becomes gelatinous, and in section appears as a thin layer stained faintly with gentian violet, and is colorless in haematoxylin; there is a slight shrinkage of the protoplast from the wall. Then, on the periphery of the protoplast, cleavage furrows appear (fig. 31). These furrows are at first broader at the periphery, but become narrower as they cut through the protoplast, appearing as fine lines, but finally become the same width throughout their extent. They follow a curved

path through the protoplast and isolate small regions of the cytoplasm, each with a nucleus and a pyrenoid fragment. In this way the entire contents of the mother cell is cleft into uninucleate masses. These delimited protoplasts then become angular, later round off somewhat, and finally elongate before liberation.

The liberated zoospores are from 2 to 6 microns in length and from 2 to 3 microns in diameter. They are oval to fusiform in shape (figs. 6, 13, 19, 36–38), and are biciliate, the cilia arising from a disc-shaped blepharoplast at the anterior end of the cell (figs. 36–38). The motile apparatus is easily observed after treatment with osmic acid and staining with acid fuchsin. The cilia are approximately equal in length to the body of the zoospore. They curve out from the point of attachment in the form of a narrow **U**. The chromatophore is a parietal band running half way around the cell, and it may be occasionally broader at the posterior end. At the posterior end of the chromatophore is a small pyrenoid which may show a very delicate starch sheath. The nucleus lies in the colorless cytoplasm nearer the anterior end of the cell. I have been unable to observe a rhizoplast connecting the nucleus and blepharoplast, as Kater (1929) reports in *Chlamydomonas nasuta*, and Timberlake (1902) for swarm spores of *Hydrodictyon*. At the anterior end of the chromatophore there is imbedded a small lenticular stigma and I have also seen one or two small, refractive droplets, but because of the minuteness of the zoospore I have been unable to see if they pulsate; contractile vacuoles have been reported in the zoospores of *Cladophora*, *Chlamydomonas*, etc. I have observed variation in the shape of the zoospore, motile protoplasts with two pairs of cilia (the cilia at opposite poles), two chromatophores, stigmata and nuclei, occurring probably as a result of irregular cleavage.

The literature and phenomenon of cleavage and spore formation have been extensively reviewed by Harper (1899) and more recently by Schwarze (1922). The former describes and figures spore formation in *Synchytrium decipiens*, *Pilobolus*, and *Sporodinia* as a process of progressive cleavage. Subdivision of the initial sporangial cell to form spores, in each case, is accomplished by surface furrows which cut through the spore plasm, cleaving it into smaller portions until the spores are cut out. In *Synchytrium* and *Pilobolus* Harper points out that the uninucleate protoplasts which at first are delimited represent only a phase of the cleavage process. These protospores, as he calls them, enter upon a period of growth, during which the single nucleus multiplies to form many. Nuclear multiplication is followed in the case of *Synchytrium* by the formation of walls about the protoplasts, which now round off and are ready for distribution. In *Pilobolus* the period of nuclear multiplication is followed by cell division

through constriction, which results in the ultimate formation of binucleate spores. Cleavage in *Sporodinia* results in the cutting out of multinucleate protoplasts which round off and develop walls and are immediately ready for distribution as sporangiospores; the process in *Sporodinia* is more abbreviated than in *Synchytrium* or *Pilobulus*. Zoospore formation in *Chlorococcum infusionum* shows similarity to the process described by Harper in the sporangia of *Sporodinia*, but in *Chlorococcum* the cleavage furrows delimit *uninucleate* segments, which are distributed as zoospores.

Behavior of the zoospores. As noted above, the zoospores are finally set free into the surrounding medium, and enter upon a period of motility which is of surprising length, in view of the observations on the motile cells of other forms. West (1916) states that the length of motility is usually not more than several hours. Hazen (1899) found that the microzoids of *Sphaerella lacustris* were motile only through the day on which they were formed. (These, however, have since been found to be gametes.) I have observed the zoospores of *Chaetomorpha aerea* to be motile for not over six hours. The zoospores of *Chlorococcum infusionum* may retain their motility for periods in excess of thirty-six hours.

Light plays an important rôle in the direction of zoospore motility. If hanging drop cultures containing motile zoospores are darkened, motility ceases almost completely, being confined to very feeble movement of individuals in a small area, but if these cultures be returned to the light, the zoospores again enter on a period of rapid movement, always concentrating at a point nearest the source of illumination.

Temperature is an important factor in the liberation of zoospores from the zoosporangia. Other conditions being the same, a slight change in temperature, either from a lower to higher, or vice versa, is a sufficient stimulus to cause the spores to be set free. For example: hanging drop cultures containing zoosporangia, in 0.2 per cent Knop's solution, were grown in a north window at from 18° to 19°C. under a microscope to permit continuous observation. At the time of examination, 3:05 p.m., no zoospores were swarming. The microscope with the culture was then moved further away from the window, to a position where the temperature was from 21° to 22°C. Within three minutes after changing the position of the culture, or at 3:08 p.m., several sporangia burst simultaneously, and within fifteen minutes the entire drop was full of swarming zoospores which had been liberated. From numerous experiments similar to the one described above I have concluded that a slight deviation from the temperature in which the culture is growing is sufficient to effect liberation of swarm spores. In the same way liberation of zoospores occurs when cultures containing zoosporangia are transferred from a warmer to a cooler temperature. Similar observations were long ago reported by Klebs (1896).

The influence of the concentration and composition of the nutrient medium on zoospore and aplanospore formation have long been known. Faminztin (1871), Artari (1892), and Klebs (1896) agree that solutions of low nutrient concentration result in continuous multiplication by zoospores, and that in solutions of higher nutrient content non-motile spores or aplanospores are formed. I have been able to confirm Famitzin's and Artari's observations on the influence of nutrient concentration on the method of reproduction in *Chlorococcum infusionum*. It is beyond the scope of this paper to describe in detail experiments of the above nature, but I consider it of interest to report briefly a few observations. Hanging drop cultures with various solutions were innoculated with cells from a rather dry agar culture in which numerous aplanosporangia and vegetative cells were present. The cultures were grown in a north window at a temperature of from 18 to 20 degrees, and frequently examined; all cultures were started between 11 and 11:15 a.m.; three cultures each were made in distilled water, 0.35 per cent Knop's solution, and 3.0 per cent Knop's solution. Immediate examination showed that in all the cultures some aplanospores were liberated and began to swarm as zoospores. In distilled water and in 0.35 per cent Knop's solution, more zoospores were swarming than in the 3.0 per cent solution. The last of the zoospores in the 3.0 per cent solution became quiescent within four hours; those in 0.35 per cent Knop's solution became quiescent within 13 hours, and those in distilled water only after 30 hours. Examination of the cultures on the following evening, i.e., about 32 hours later, showed interesting variations. Cultures in distilled water showed a second liberation of motile bodies. They also showed that almost every vegetative cell was undergoing cleavage for the formation of zoospores. Those with 0.35 per cent Knop's solution contained a few zoospores recently liberated and many vegetative cells undergoing cleavage. The cultures in 3.0 per cent solution were characterized by the absence of any motile cells; those zoospores which were liberated the day previously had grown somewhat. No cleavage was apparent in the vegetative cells. Repeated examinations of the cultures revealed that on the third, fourth, and fifth days successive liberations of zoospores and cleavages occurred in distilled water, the zoosporangia, and consequently the zoospores, becoming smaller. The quiescent zoospores set free on the previous days, showed very little increase in size. In cultures with 0.35 per cent solution fewer cells showed cleavage, but a relatively high number of zoospores were set free on the third, fourth, and fifth days; zoospores liberated on previous days showed some growth, those set free on the first day having attained almost the size of mature vegetative cells by the fifth day. Cells in the 3.0 per cent nutrient solution neither formed nor liberated zoospores after

the first day. Cleavage proceeded quite rapidly and was widespread, but the cleavage products developed thick cellulose and thick gelatinous membranes, and either were not liberated or were liberated without a motile stage. The zoospores set free the first day in these cultures had by the fifth day increased to the size of mature vegetative cells. I have grown the plants, in similar experiments, in solutions ranging in concentration from distilled water and a 0.1 per cent solution to a 4.0 per cent solution, and find that in solutions of less concentration than 1.8 per cent reproduction is primarily by means of motile zoospores, and in solutions higher than 1.8 per cent reproduction is by means of non-motile aplanospores. There is no sharp distinction to be drawn in media whose concentration closely approaches 1.8 per cent from either direction. In these concentrations both methods of reproduction are met with; I have observed that as the solution approaches the maximum concentration for zoospore production, and conversely as the concentration approaches the minimum for aplanospore production, formation of both types of reproductive cells becomes equally frequent. These observations confirm those of Famintzin (1871, p. 51) who states:

> Der Concentrationsgrad der Flüssigkeit ist von grossem Einflusse auf der Entwickelung der Algen. In der sehr diluirten, deren Concentration nicht ein Procent übertrifft, wird, bei den von mir untersuchten Algen, dem *Chlorococcum infusionum* und dem *Protococcus viridis*, die Vermehrung nur durch Zoosporen zu Stande gebracht; die ausgeschwärmten Zoosporen erzeugen wieder Zoosporangien und so fort; . . . In der 2% Salzlösung oder ein höheren Concentration wird die Zoosporenbildung gehemmt; die Vermehrung dagegen durch Zerfallen in unbewegliche Kugeln vermittelt. Versetzt man diese Algen in Salzlösungen von einer geringeren Concentration als 2%, so tritt die Zoosporenbildung wieder ein; steigert man dieselbe auf 2%, so wird sie wiederum gehemmt.

Further development of the zoospores. After variable periods of motility the zoospores come to rest, lose their cilia, secrete the outer gelatinous wall membrane, and begin their development into vegetative cells. In hanging drop cultures, as noted above, the zoospores always come to rest near the margin of the drop (figs. 5, 6). In large, flat culture dishes a film of zoospores is formed on surface of the culture liquid. In drop cultures with a large number of zoospores, when concentration of them takes place at the edge of the drop, it often happens that they burst through the original boundary of the water and establish themselves in a small surface film which is continuous with the water of the original drop (fig. 5). When one or several zoospores have reached the edge of the drop, an attraction seems to be set up at that point. Other swarmers swim to the same place and come to rest, at first forming a single line, radiating in from the edge of the

drop, their anterior ends pointing to the margins. Other zoospores swim to the same place and force themselves at least part way between those already settled, until finally they give the appearance of an intricate mosaic (fig. 6), this process giving rise to the expanses of angular cells found at the surface of cultures (figs. 7–10). This angular condition of *C. infusionum* was described by Kützing for *Limnodictyon Roemerianum*.

This type of aggregation into a cellular expanse may be properly termed a loose coenobium. It is possible that the morphogenetic aggregation of swarm spores of *Hydrodictyon* and *Pediastrum* into definite patterns may have originated in such a simple way as this. During the course of their development these young cells never achieve the spherical form unless they become separated.

As the developing zoospores increase in size, they become angular by compression (figs. 6, 8, 9), and as growth continues the typical angular coenobium is formed. It is important to note that no cell division by bipartition occurs; the association of the cells into coenobia is entirely determined by the original position assumed by the zoospores as they become quiescent, and their ensuing increase in size. During the growth of the young cells, the chromatophore, which in the zoospore only partially covers the surface of the protoplast, is extended so that it is either entirely continuous or almost continuous. Figures 13–18 represent a series of stages in the metamorphosis of a zoospore into a mature vegetative cell. The chlorophyl-bearing area is gradually extended until only a small colorless region remains (fig. 18), and as the cell ages, the outer gelatinous membrane becomes considerably thickened.

In nutrient solutions the entire life cycle from zoospore to zoospore occupies between five and six days.

Multiplication by aplanospores. Miss Bristol (1920), Artari (1892), and Famintzin (1871) describe and figure non-motile gonidia for *Chlorococcum humicolum* and *C. infusionum*. They are produced usually in solutions of high concentration, in drier environments, and, in general, under conditions unsuitable for zoospore production. I find them occurring most frequently in *C. infusionum* in drying agar cultures. They represent, at least in this case, zoospores which of necessity have omitted a motile stage, and they complete their development without it. They originate by the internal cleavage of a vegetative cell, in the same manner as zoospores. However, after cleavage, the daughter protoplasts round off and may become ellipsoidal, developing cell membranes almost as thick as those of the mother cell (fig. 22). The development of this rather thick cell wall and the spherical to ovoidal shape immediately distinguish them from zoospores. As the aplanospores begin to grow the mother cell wall bursts and

they are set free, whereupon they enlarge and develop into mature cells. They may enlarge considerably before liberation, and may themselves cleave into aplanospores. In this way cell complexes composed of several generations are built up.

Conjugation of zoospores has been observed and described in *Chlorococcum humicolum* by Bristol (1920), and Puymaly (1924); neither Famintzin (1871) nor Artari (1892) observed conjugation of zoospores in *C. infusionum*. Fritsch (1927), maintaining that in the simpler members of the Chlorococcales there are no strong sexual tendencies, notes that only one case of anisogamy (*Phyllobium*) and none of oogamy have been reported in the entire group.

In attempting to produce conjugation of zoospores, I have repeated the methods employed by Klebs (1896) in his studies on *Chlamydomonas*. Abundant zoospores were produced, but in every case they began to develop without conjugation. Material from different cultures was brought together in view of claims that zoospores from the same sporangia or cultures never fuse. In my opinion either fusion does not occur in nature in this species, or I have failed to reproduce in artificial culture the conditions necessary for fusion. A further possibility might be suggested—that we are here dealing with a heterothallic species, that is one in which the gametes must be produced by strains or clons of widely separate origin, as recently described by Strehlow (1929) for *Chlorogonium*, and by several other investigators for other genera. Reproduction in *C. infusionum* in so far as I have been able to observe seems to be a process of vegetative multiplication, either by the formation of zoospores which develop without conjugation, or by non-motile aplanospores.

SUMMARY

1. Prolonged observations of cultures show that *Chlorococcum infusionum* (Schrank) Meneghini is identifiable by the following characters: the aggregation of polyhedric individuals into a loose coenobium which originates during the swarming of the zoospores; mature vegetative cells vary in size from eight to thirty microns in diameter. The wall is composed of an inner, thin, cellulose layer adjacent to the protoplast, and an outer gelatinous layer, which is often thick and lamellate. The chromatophore is parietal, with or without an opening, and often contains numerous droplets of colorless oil; the chromatophore contains one or occasionally two angular or spherical pyrenoids. The cells are uninucleate, becoming multinucleate only immediately preceding cleavage.

2. Multiplication is by formation of biciliate zoospores and non-motile aplanospores, both of which arise by progressive cleavage of a mother

protoplast into uninucleate segments. The pyrenoid of the mother cell fragments during cleavage, each daughter protoplast receiving a fragment which becomes a pyrenoid; there is no evidence for an origin *de novo* of the pyrenoid. Zoospores and aplanospores increase in size to form the vegetative cells.

3. There is no increase in number of individuals by cell bipartition.

4. Gamete fusion has not been observed. Apparently it does not occur in nature or else conditions in artificial culture are an impediment to fusion.

5. Environmental factors, as Klebs and others have shown, influence the formation, behavior, and development of zoospores and aplanospores.

(a) Multiplication is by zoospore formation as long as the moisture is sufficient to permit their escape from the zoosporangium. In dry cultures the potential zoospores develop thick gelatinous membranes and begin their development without a motile stage.

(b) In solutions of lower concentration than 1.8 per cent, zoospore formation proceeds rapidly; in nutrient solutions of greater concentration multiplication is by aplanospores.

(c) Slight changes in temperature cause liberation of zoospores.

6. The pyrenoid is associated with starch formation. Segments are separated from the protein core, dissolve, and are deposited in the form of starch in the cytoplasm surrounding the pyrenoid. It is suggested that the chemical view of certain proteins as complex molecules which have carbohydrate side chains may be the basis of the morphological changes taking place in the pyrenoid during starch formation. The so called 'stroma starch' is in the form of minute ellipsoidal grains which are cleft off from the starch ring surrounding the pyrenoid, and migrate radially through the chromatophore.

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Note. Since the final proof of this paper was read, I have had an opportunity to examine pure cultures of three species of *Chlorococcum*, namely *C. humicolum*, *C. infusionum*, and *C. Wimmeri*, from the Pflanzenphysiologisches Institut der deutschen Universität in Prague (see PRINGSHEIM, E. G. Algenreinkulturen. Ber. Deutsch. Bot. Gesell. **47:** 530–535. 1929). It is therefore of interest to report that the organism I have isolated and identified as *C. infusionum* appears to be identical with this European culture of *C. infusionum* isolated by F. Mainx.—H. C. B.

Description of plates 32–36

All of the figures were drawn with the aid of a Zeiss drawing apparatus, using a Zeiss apochromatic objective 2 mm, N.A. 1.30 and compensating oculars 15× and 20×. The approximate magnification of each figure is given.

Plate 32

Fig. 1. Two months old culture on 0.2 per cent Knop's agar.

Fig. 2. Six months old culture on 0.3 per cent Knop's agar.

Fig. 3. Twenty-two months old culture on 0.3 per cent Knop's agar.

Fig. 4. Young colony from the surface of a Petri dish culture on 0.2 per cent agar. ×85.

Fig. 5. Zoospores bursting through the margin in a hanging drop culture, three hours after motility ceased. ×110.

Fig. 6. The same, enlarged. ×750.

Plate 33

Fig. 7. Portion of a colony from an old agar culture, numerous ripe zoosporangia. ×750.

Fig. 8. Developing zoospores becoming angular by compression. ×750.

Fig. 9. Portion of the surface film of a liquid culture. ×330.

Fig. 10. Developing zoospores thirty-six hours after swarming; free cell surfaces curved, adjacent cell surfaces flattened. ×750.

PLATE 34

Fig. 11. Vegetative cell with opening in chromatophore near the pyrenoid; outer cell membrane thick and faintly lamellate. ×3000.

Fig. 12. Vegetative cell with thick wall, after treatment with sulphuric acid and iodine; the protoplast has shrunken from the cellulose wall (represented as granular): the lamellar structure of the outer gelatinous membrane becomes apparent—partially schematic. ×3000.

Figs. 13–18. Stages in the development of a zoospore into a mature vegetative cell. ×3000.

Fig. 19. Zoosporangium with four zoospores. ×3000.

Fig. 20. Large zoosporangium which contained approximately forty-three zoospores. ×3000.

Fig. 21. Escape of zoospores in a gelatinous vesicle. ×3000.

Fig. 22. Aplanosporangium with aplanospores. ×3000.

PLATE 35

Fig. 23. Vegetative cell fixed in corrosive sublimate which differentiates the plastid: 'stroma starch' grains present. ×2175.

Fig. 24. Vegetative cell with vacuolate cytoplasm. ×2175.

Fig. 25. Vegetative cell: the enlarged nucleus in spireme stage. ×2175.

Fig. 26. Vegetative cell with 'stroma starch' grains. ×2175.

Fig. 27. Vegetative cell immediately prior to cleavage for zoospore production. Minute nuclei present near the periphery of cell. ×3000.

Figs. 28–30. Fragmentation of the pyrenoid body and dispersal of fragments in the cytoplasm. ×3000.

Fig. 31. Formation of surface furrows which extend toward the center, isolating unincleate segments with a pyrenoid fragment. ×3000.

Fig. 32. Partial section of an almost mature zoosporangium; the cleavage products have elongated. ×3000.

Fig. 33. Complete section of an almost mature zoosporangium; (cytoplasm omitted in some zoospores for clarity). ×3000.

Fig. 34. Section of a smaller zoosporangium showing six zoospores. ×3000.

Fig. 35. Young vegetative cell developing from zoospore. ×3000.

Figs. 36–38. Face, lateral and end views of zoospores fixed in osmic acid. Nucleus, pyrenoid, starch grains, cilia, and blepharoplast visible. ×3000.

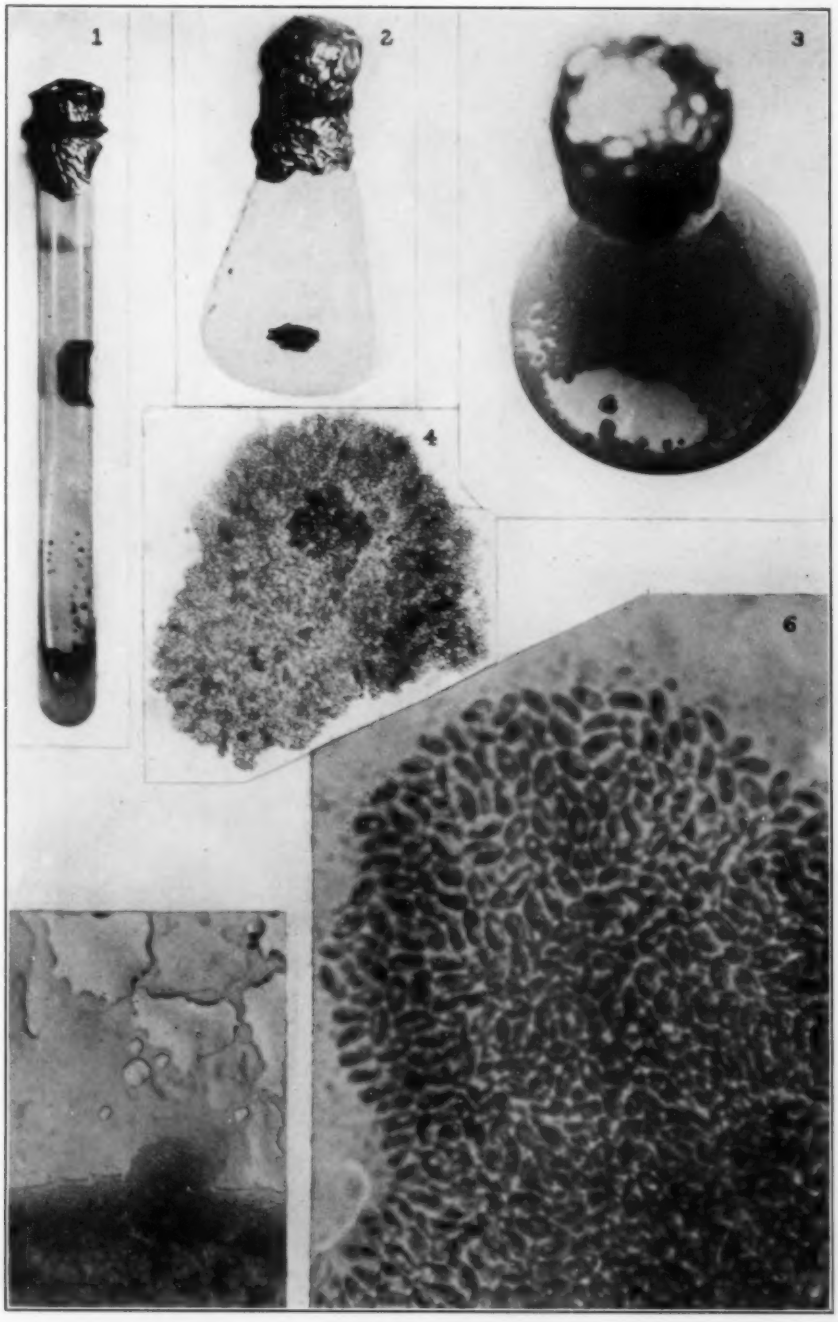
PLATE 36

Figs. 39–47. Various appearances of the pyrenoid during starch formation. Explanation in text. ×4300.

Fig. 48. Section of vegetative cell showing 'stroma starch' and its origin from the starch ring about the pyrenoid (nucleus not present in section). ×4300.

Fig.s 49–56. Appearances of pyrenoid during starch formation. Explanation in text. ×4300.

Figs. 57–59. Loss of staining reaction by pyrenoids in cells from darkened cultures. ×4300.



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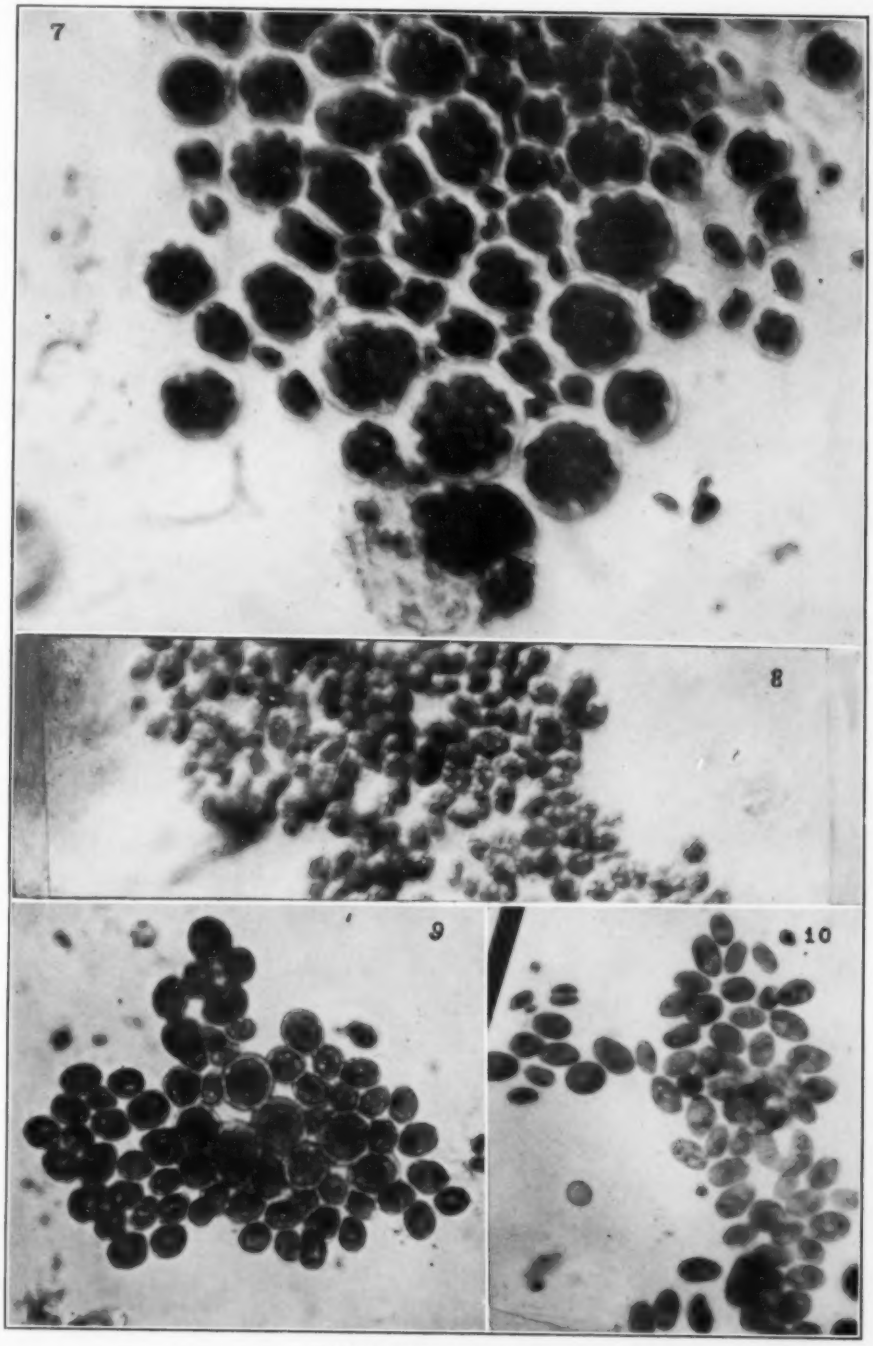

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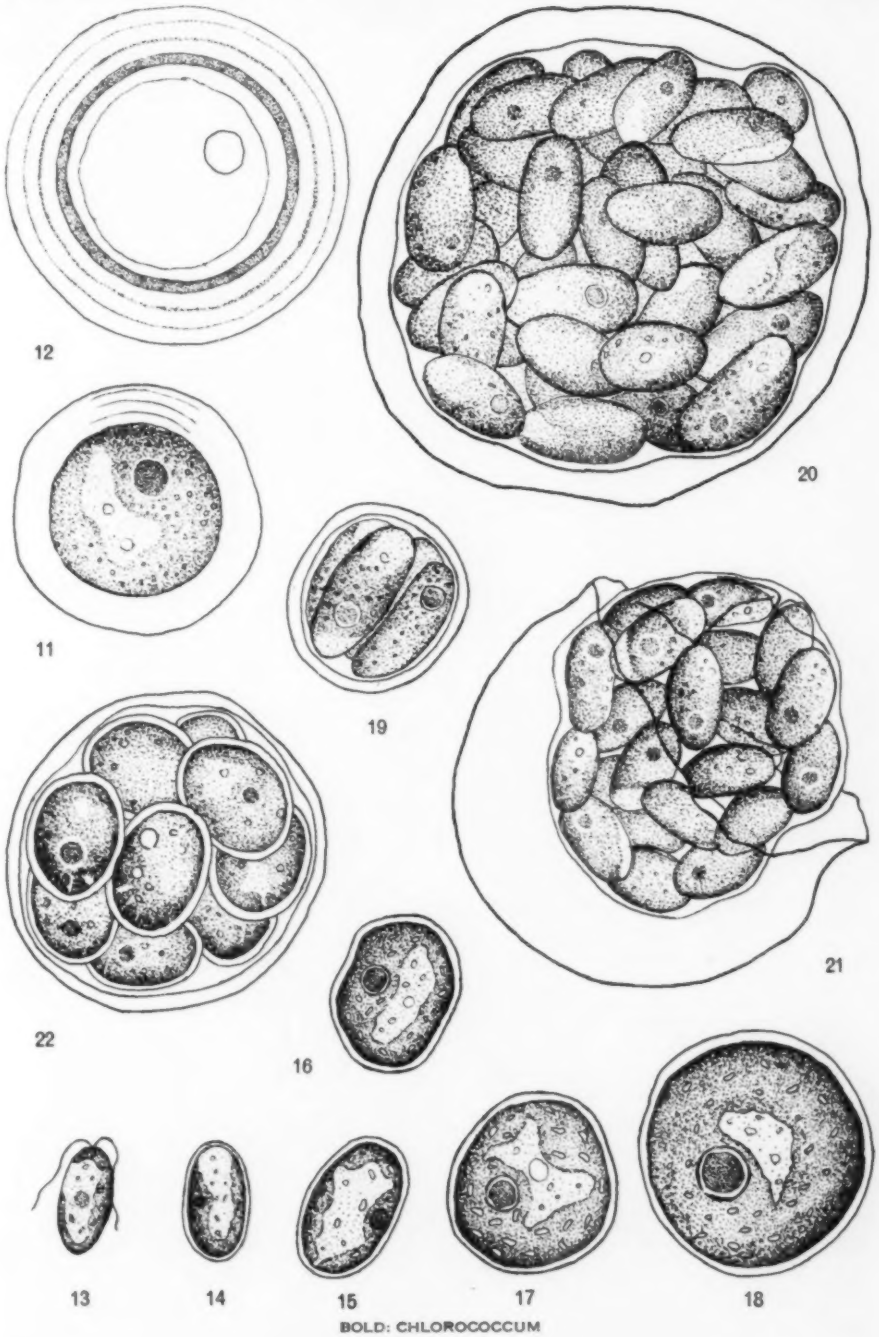

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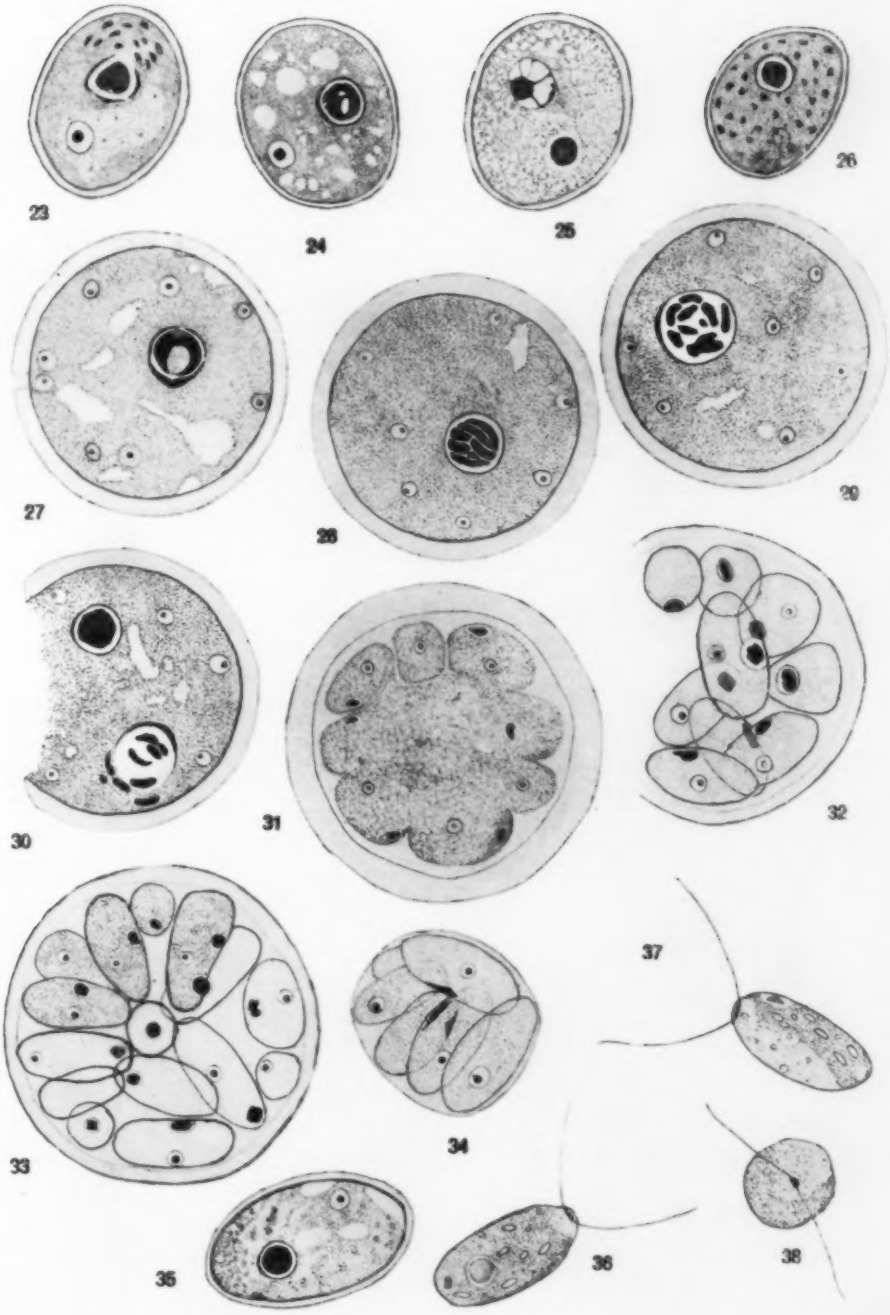

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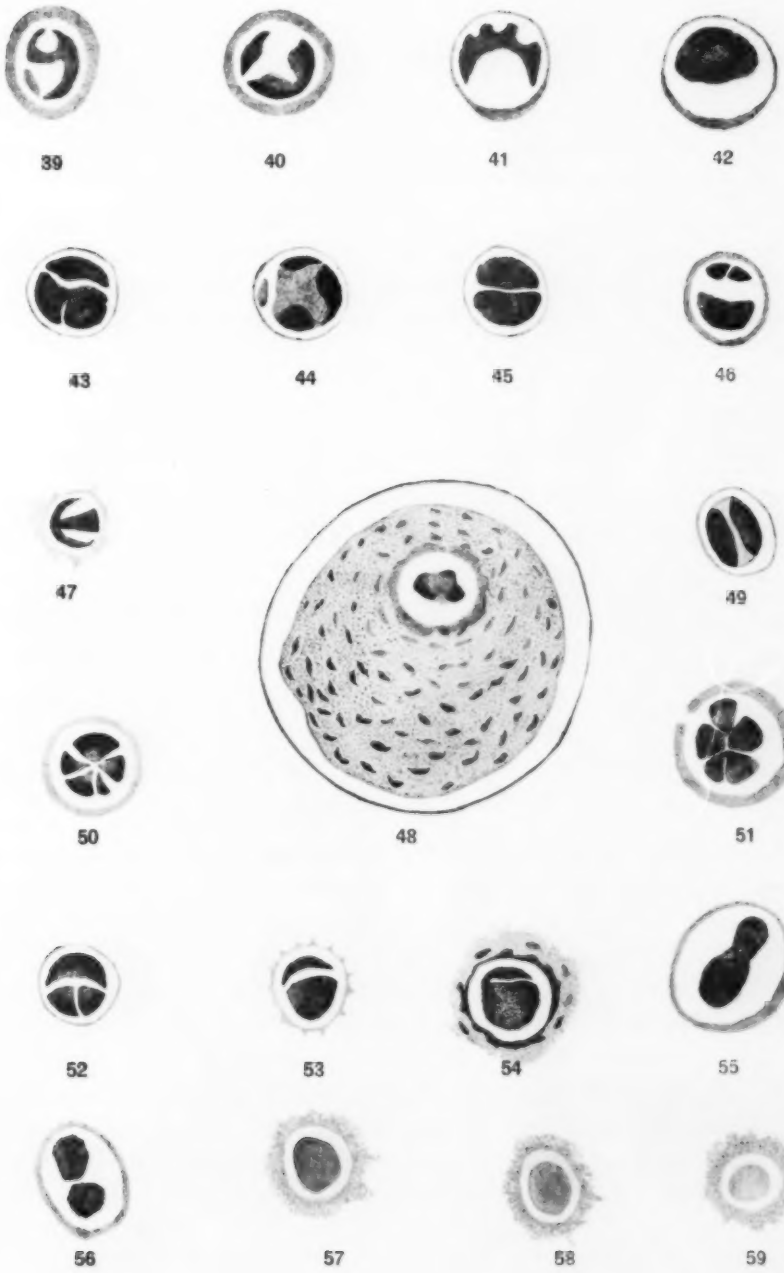

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Notes on the algae of Uruguay

MARSHALL A. HOWE

(WITH PLATE 37)

Beginning in 1907, Dr. Florentino Felippone of Montevideo has sent to the writer small collections of Uruguayan algae, chiefly marine, for determination. In the following list, 22 species, including one that is described as new, are recognized, and one specimen is referred to genus only. It is not a long list, but, as it is apparently the first to be published for Uruguay alone, it may have a certain interest for specialists in this line. The species seem to be more or less indentical with those of southern Brazil.

CHLOROPHYCEAE

CLADOPHORA FRACTA (Vahl) Kütz.

In fresh water, Montevideo, nos. 1252, 1264, and 1265.

CLADOPHORA FRACTA SUBSIMPLEX Kütz.

Montevideo, no. 1277. Other species of *Cladophora* occur in Felippone's collections.

RHIZOCLONIUM HIEROGLYPHICUM (Ag.) Kütz.

In fresh water, Montevideo, no. 1850.

ULVA LACTUCA L.

Cabo de Santa Maria, Rocha, nos. 1826 and 1855, Punta del Este, nos. 1840 and 1841 (thallus 45–50μ thick).

ENTEROMORPHA COMPRESSA CONSTRICTA J. Ag.

Costa Sur, no. 117, Isla de Flores, nos. 135 and 1825, Costa Maldonado, no. 276. In reporting these numbers to the collector, Dr. Felippone, the writer referred no. 1825 to *Enteromorpha Linza* and the others to *E. intestinalis*. Though some of these specimens have much the habit of *E. Linza* and cross sections of the thallus resemble the figures of sections of that species, as published by J. Ag. (Till Alg. Syst. **3**: 138. 1883), the two laminae of the broader parts of the thallus separate more readily than those of *E. Linza*, and many of the plants are freely proliferous from the basal margins. The expanded upper parts of thallus occasionally attain a width of 5 cm., resembling and even surpassing in this respect no. 123 of Areschoug's Algae Scandinavicae Exsiccatae, which J. Agardh appears to make the type of his form *constricta*.

No. 1276 (84,687) of Herter's Plantae Uruguayenses, from Punta del Este, Maldonado, distributed as *Enteromorpha compressa* (L.) Grev., evi-

dently belongs with the forma *constricta*, but no. 731 of the Kryptogamae Exsiccatae of the Vienna Museum, from 'prope urbem Montevideo', is nearer what currently passes as the typical *E. compressa*. Herter's no. 1274 (84,685), from Punta del Este, issued as *Enteromorpha compressa*, var. *procerrima* Kütz., is filiform, scarcely compressed, and its branches arise irregularly (not distichously) and most of them taper very little towards the base. This we are disposed, for the present, to refer to *Enteromorpha prolifera* rather than to *E. compressa*. The plants are only 3–5 inches long, while Kützing ascribes a length of 2–3 ft. to his forma *procerrima*.

ENTEROMORPHA PROLIFERA (O. F. Müll.) J. Ag.

Species of *Enteromorpha* are notoriously difficult to define. We are inclined to refer to *E. prolifera* rather than to *E. compressa* Dr. Felippone's no. 1845 from Montevideo, as well as Herter's no. 1274 from Punta del Este, mentioned above.

BRYOPSIS PLUMOSA (Huds.) Ag.

Punta del Este, no. 1149. A small delicate form.

OEDOGONIUM sp.

Punta Gorda, no. 1249.

CODIUM DECORTICATUM (Woodw.) M. A. Howe

(?) *Codium decumbens* Mart. Fl. Bras. **1**: 19. 1833.

Isla de Lobos, no. 30, and one without number; Maldonado, no. 282; Isla de Flores, no. 286; Punta del Este, no. 1829; Cabo de Santa Maria, no. 1861, without locality.

The peripheral utricles range from 160μ to 500μ in maximum diameter, with most of them 220 to 350μ; they are rounded-truncate or blunt and are thin-walled. Some of the specimens (notably no. 286) agree well with O. C. Schmidt's description (Bibl. Bot. **91**: 58) of one of two apparently authentic, though not technically typical, specimens of *Codium decumbens* Mart. seen by him in herb. Hamburg, and referred by him to *C. lineare* Ag. However, there is little in the habit of most of them to suggest either of the descriptive words *decumbens* or *lineare*. The thallus in nearly all has the appearance of being flattened, at least under the dichotomies.

RHODOPHYCEAE

PORPHYRA MINOR Zanard. (?)

On *Gelidium corneum*, Cabo de Santa Maria, Rocha, nos. 1858 and 1874. Both plants are monostromatic, 22–40μ thick; one (no. 1858) is suborbicular-flabelliform, 8.5 cm. broad and 6.5 cm. high; the other (no. 1874) is

linear-oblong, 4 cm. by about 7 mm. The former is fertile, monoicous; 8 spores in a sporocarp; antheridia in small patches among the sporocarps, 32 antherozoids to an antheridium; vegetative cells occurring rarely among the sporocarps. Both *Porphyra minor* and *P. microphylla* were described by Zanardini as occurring on *Gelidium corneum* in the Adriatic Sea. Both were sterile or, at least, the reproductive parts were not really described. Both of the Uruguay plants are larger than either *Porphyra minor* or *P. microphylla*, which are described as only 1.5 cm. high or less. *Porphyra vexillaris* Mont., described a few years later than *P. minor* as an epiphyte on *Grateloupia filicina* from Martinique, is much smaller, being only 2–4 mm. long.

GELIDIUM CORNEUM (Huds.) Lamour.

Numerous specimens from various localities, notably Punta del Este, Cabo de Santa Maria, Isla de Flores, and Isla de Gorriti; also, in Herter's Plantae Uruguayenses, no. 1272 (84,683), from Punta del Este. Some of the specimens represent coarser forms of the species, more or less approaching *Gelidium cartilagineum*.

GIGARTINA TEEDII (Roth) Lamour.

Isla de Flores, nos. 134 and 136; Punta del Este, nos. 1167, 1833, 1835, 1844, and 1848a. Several of the specimens are cystocarpic. Previously reported from Brazil.

GIGARTINA ELEGANS Grev.

Isla de Flores, no. 192; Punta del Este, no. 1834. This species is evidently closely allied to *Gigartina Teedii*, but differs somewhat in habit, being more finely dissected and the ultimate ramuli more substellate-glomerate. Original specimens from southern Brazil (playa de Aldea Velha, Prov. Espiritu Santo) are preserved in herb. Greville in Edinburgh and in the Muséum d'Histoire Naturelle in Paris. A photograph of the Greville specimen—the technical type, though rather less *elegant* than the specimens in Paris—is published herewith (figure 1).

GYMNOGONGRUS GRIFFITHSIAE (Turn.) Mart.

Isla de Flores, nos. 138, 181, and 193. Reported from southern Brazil by Martius (Fl. Bras. **1**: 27. 1833).

ACTINOCOCCUS AGGREGATUS Schmitz.

On *Gymnogongrus Griffithsiae*, Isla de Flores, nos. 138 and 181. Rosenvinge (Kgl. Danske Vidensk. Selsk. Biol. Medd. 8^4: 1–40. 1929) has shown conclusively that *Actinococcus subcutaneus* is the tetrasporic phase of *Phyllophora Brodiaei*, in and on which it grows in a peculiar sort of parasitism,

without the intervention of a true cystocarp. It is quite possible that a similar relation exists between *Actinococcus aggregatus* and *Gymnogongrus Griffithsiae*.

AHNFELTIA PLICATA (Huds.) Fr.

Isla de Lobos, no. 28; Isla de Gorriti, no. 195.

The specimens, especially no. 195, are somewhat coarser than the European and North American representatives of this species and the cortical filaments are also somewhat coarser. In size it approaches the more slender forms of *Ahnfeltia Durvillaei* (Bory) J. Ag., which ranges from Peru to the Cape Horn region. *A. plicata* has been reported from Brazil, Falkland Islands, and Tierra del Fuego.

HYPNEA MUSCIFORMIS (Wulf.) Lamour.

Punta del Este, no. 1848b.

This species occurs also in Brazil.

CRYPTOPLEURA FIMBRIATA (Grev.) Kylin, Lunds Univ. Årsskr. II. **20**[6]:92. 1924.

Nitophyllum fimbriatum Grev. St. Hil. Voy. Dist. Diam Brésil **2**: 447. 1833. J. Ag. Sp. Alg. **3**[3]: 70. 1898.

Nitophyllum calophylloides J. Ag. Till Alg. Syst. **4**: 68. 1885.

We have seen the following specimens from Uruguay collected by Dr. F. Felippone: Costas de Maldonado, no. 97; Puerto de la Paloma, Rocha, no. 961; Punta del Este, no. 1828 and 1829b; Cabo de Santa Maria, Rocha, nos. 1860, 1862, 1864, 1876, 1878, and 1880; and also W. Herter's Plantae Uruguayenses no. 1289 (85,089) from Puerta de la Paloma, distributed by Herter under the name *Nitophyllum Curdieanum*, which belongs to an Australian species. It sometimes grows attached to *Gelidium corneum* and to *Codium decorticatum*. These specimens exhibit a considerable variety of form and texture, but we believe they represent a single species. Notable is their rather firm texture as compared with most of the members of the genus. The fronds are for the most part composed of three or more layers of cells except for a narrow unistratose margin. This margin is about 75–80μ thick, while most of the frond is 100–160μ thick, sometimes rising to 275μ in the more or less well-defined midrib of the major segments. The original specimen of *Nitophyllum fimbriatum* Grev. was collected near Aldea Velha, Brazil, by St. Hilaire. The type specimen (figure 2) in the Greville Herbarium is antheridial. The antheridial sori, like the tetrasporangial, are sometimes within the margin of the larger divisions of the frond but they more commonly occupy small marginal proliferations of great diversity of form. The antheridial appendages, which doubtless suggested

the specific name, are notably crispate. The cystocarps, which are 0.75–1.25 mm. in diameter and somewhat unequally protuberant on the two faces of the frond, are usually on the larger segments, but are sometimes also on small marginal proliferations.

CHONDRIA DASYPHYLLA (Woodw.) Ag.

Punta del Este, no. 1846.

POLYSIPHONIA VIRGATA (Ag.) Spreng.

Punta del Este, no. 1847; and Cabo de Santa Maria, Rocha, nos. 1865 and 1882. Type from the Cape of Good Hope. Reported from Brazil by Martius (Fl. Brasil. **1**: 16. 1833) under the name of *Corradoria complanata*. The specimens differ among themselves considerably in habit and they are rather smaller than South African specimens seen.

Callithamnion Felipponei M. A. Howe, sp. nov.

Fronde epiphytica, 1–3 cm. alta, virgata et subsimplici vel cum ramis paucis virgatis plus minusve basalibus; caulibus praecipuis corticatis fasciculos ramulorum ecorticatorum monosiphoniorum dense vel aliquando sparse ordinatos, cristatos vel alopecuroideos, strictos vel erecto-patentes ferentibus, ramulis cum ramellis rigidis alterno-distichis, irregulariter spiralibus, vel subdivaricate dichotomis incurvis vel aliquando recurvis acuminatis (vel aetate obtusis) 75–160μ latis in partibus majoribus, saepe ad 13μ vel minus in cellulis apicalibus, cellulis 1–2.5-plo (plerumque 1–5-plo) longioribus, parietibus 8–30μ crassis; sporangiis tripartitis, 50–60μ×40–50μ.

In *Gelidio corneo*, Uruguayae, Cabo de Santa Maria, Rocha, *Dr. F. Felippone 1866, 1869a (exemplo typico), 1873b, 1875b*, et *1877*.

Callithamnion Felipponei cum *C. Arbuscula* (Dillw.) Lyngb., incola Europae borealis, et *Ceratothamnione Pikeano*, incola orarum Americae-Borealis, comparandum est, sed a utriisque magnitudine minore, habitu simpliciori plus virgato, ramellis rigidioribus plus falcatis, parietibus crassioribus, differt.

Frond epiphytic, 1–3 cm. high, virgate and subsimple or with a few virgate branches from near base, main axes corticated, bearing densely or sometimes sparsely disposed tufted or alopecuroid, strict or erecto-patent fascicles of ecorticate ramuli, these with rigid alternate-distichous, irregularly spiral, or subdivaricately dichotomous incurved or sometimes recurved, acuminate (or, in age, obtuse) ramelli, these 75–160μ broad in older parts, often tapering to 13μ or less in apical cells, the cells 1–2.5 (mostly 1.5) times as long as broad, the cell walls 8–30μ thick; tetrasporangia tripartite, 50–60μ×40–50μ.

On *Gelidium corneum*, Cabo de Santa Maria, Rocha, Uruguay, Felippone, nos. 1866, 1869a (type, figure 3), 1873b, 1875b, and 1877.

Callithamnion Felipponei is evidently related to *C. Arbuscula* (Dillw.) Lyngb. of northern Europe and *Ceratothamnion Pikeanum* of the Pacific coast of North America, but manifestly differs from both in its smaller size, in the simpler more virgate habit of the plant as a whole, and in the more rigid, more falcate, thicker-walled ramelli. Until one sees the tetrasporangia, it suggests certain species of *Dasya* rather more than the genus *Callithamnion*.

GRATELOUPIA FILICINA (Wulf.) Ag.

Punta del Este, no. 1842, Cabo de Santa Maria, Rocha, nos. 1863, 1870, 1872, and 1879.

GRATELOUPIA CUNEIFOLIA J. Ag.

Cabo de Santa Maria, Rocha, nos. 1856 (tetrasporic) and 1857 (cystocarpic). Type from La Guayra.

CORALLINA OFFICINALIS L.

On *Gelidium corneum*, Cabo de Santa Maria, Rocha, no. 1875a. A small slender form, about 2 cm. high. Referred to *C. granifera* Ell. & Soland. var.(?) in or iginal report to Dr. Felippone. Also, Herter's Plantae Uruguayenses no. 1265 (84,676), from Punta del Este.

AMPHIROA BEAUVOISII Lamour.

Punta del Este, no. 1831, Puerto de la Paloma, Rocha, nos. 21 and 23, also, Herter's Plantae Uruguayenses, no. 1268 (84,679), from Punta del Este, distributed as *Amphiroa foliacea* Lamour., a different species, primarily from the Pacific islands. *A. Beauvoisii* was originally described from the Mediterranean Sea.

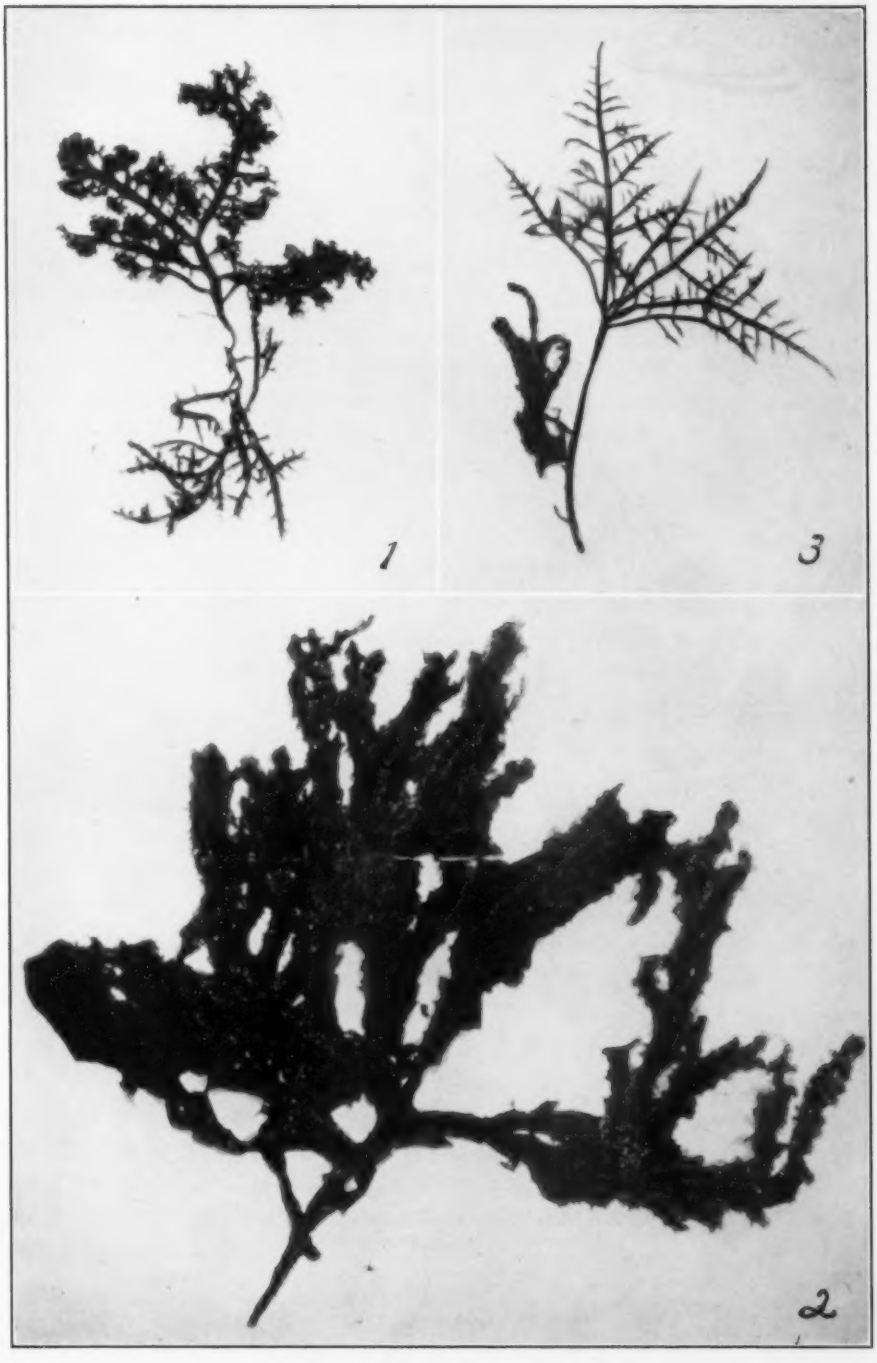
THE NEW YORK BOTANICAL GARDEN

Explanation of plate 37

Fig. 1. Photograph of the type specimen of *Gigartina elegans* Grev., from Aldea Velha, Brazil,—natural size.

Fig. 2. Photograph of the type specimen of *Nitophyllum fimbriatum* Grev., from Aldea Velha, Brazil,—natural size.

Fig. 3. Photograph of the type specimen of *Callithamnion Felipponei* M. A. Howe (*Felippone 1869a*), on *Gelidium corneum*, from Cabo de Santa Maria, Rocha, Uruguay, —natural size.



HOWE: ALGAE OF URUGUAY

The North American species of Orobanche, section Myzorrhiza

PHILIP A. MUNZ

(WITH PLATES 38, 39)

There is presented herewith an attempt to work out in more definite fashion than has been done heretofore, our species of the section Myzorrhiza as that section was understood by G. Beck in his monograph of *Orobanche* (Bibl. Bot. **4:** 78–85. 1890).[1] To the species listed by Beck must be added the Mexican *O. Dugesii* and *O. multicaulis*, which require the emendation of the section to include a bilobed as well as a crateriform stigma. However, the presence of the two bractlets below each flower and the 5-cleft condition of the calyx still hold.

In collecting material in this group in years past I have found it exceedingly difficult to get identification that was at all satisfactory. Unfortunately the immediate work done on this paper has had to be confined to the herbarium; and in plants as fleshy as these, herbarium specimens are not altogether satisfactory. In segregating the various entities that I recognize herein, I have based my conclusions largely on dissections and camera lucida drawings of the corollas, as well as the traditional criteria used by former workers, namely pubescence, calyx, tuberous base, and the like. It seems to me that in most cases the corolla characters are sufficiently correlated with zonal distribution and with hosts to warrant a recognition of many more varieties than has heretofore been done. Capsules and seeds have yielded no characters of use in distinguishing species.

For prosecuting this study I have had available the material in the following herbaria: University of California (C), Gray Herbarium (G), Dudley Herbarium of Stanford University (S), Herbarium of Frank Peirson of Pasadena (FP), and Pomona College Herbarium (P). I am greatly indebted to those who have so kindly loaned me the material in these collections. The letters indicated above after the herbarium names are those used in citing specimens. I am also indebted to Dr. I. M. Johnston of the Gray Herbarium and to Mr. C. L. Hitchcock of the Missouri Botanical Garden for notes and copies of original descriptions, to Dr. J. A. Comstock of the Exposition Park Museum in Los Angeles, and to Dr. Aven Nelson

[1] After this paper was submitted for publication, there appeared Beck's recent treatment of Orobanchaceae (Das Pflanzenreich 4^{261}: 1–348. 1930). Since no new combinations or names were used in the section Myzorrhiza for North American species, I have made no attempt to cite this more recent paper of Beck's among the references I have given.

of the University of Wyoming for the privilege of studying the types of *Myzorrhiza Hutchinsoniana* and *Orobanche xanthochroa* respectively. I have not had available sufficient material of the South American species to warrant including them in this paper.

KEY TO SPECIES

Stigma bilobed; throat of corolla not thrown up into definite palatal folds, the lower lip truncate at the base of the lobes; corolla-lobes tending to be broad, and narrowed abruptly into a short terminal tooth.

Plant glabrous or nearly so, the corolla yellowish and ca. 15 mm. long, the lobes inconspicuously toothed at the tip. Guanajuato, Mexico.....2. *O. Dugesii*

Plant plainly puberulent; the corolla with some purple, 15–25 mm. long, the lobes evidently toothed at the tip. Lower California and Puebla, Durango, and San Luis Potosi.....1. *O. multicaulis*

Stigma peltate-crateriform; throat of corolla with 2 well-marked palatal folds (except in no. 3), the lower lip not truncate at the base of the lobes; corolla-lobes usually rounded or narrowed gradually toward the tip.

Stems with a thickened tuber-like base, and branched above.

Calyx 1 cm. long; corolla 12–15 mm. long, yellowish with purple or brown, without palatal ridges in the throat; plant pruinose-puberulent, the inflorescence compact. Chaparral belt from central to Lower California.....3. *O. bulbosa*

Calyx 6–8 mm. long; corolla 13–19 mm. long, yellowish, with palatal ridges in the throat; plant cinereous-pubescent, the inflorescence open. On conifers in mountains from N. California to Washington and Idaho.....4. *O. pinorum*

Stems not with a thickened tuber-like base.

Flowers, especially the lower ones, on pedicels up to 2 or 3 cm. long; inflorescence often corymbose.

Lower lip of corolla spreading, 7–15 mm. long; anthers woolly-pubescent.....
5. *O. Grayana*

Lower lip of corolla erect, 4–6 (8) mm. long; anthers glabrate except in material from east of the Sierra Nevada.....6. *O. californica*

Flowers sessile or nearly so; inflorescence typically spicate; plants usually with somewhat grayish pubescence.

Corolla-lobes rounded, not pointed; anthers woolly to glabrate.....
7. *O. multiflora*

Corolla-lobes pointed, triangular; anthers usually pubescent.....
8. *O. Ludoviciana*

TREATMENT OF SPECIES

1. OROBANCHE MULTICAULIS T. S. Brandegee, Univ. Calif. Pub. Bot. 6: 361. 1916.

Several-stemmed, these simple and spicate or with few branches, puberulent, scarcely viscid; cauline bracts few, ovate, acuminate, 5–10 mm. long; flowers sessile, or lowermost on pedicels as long as 2.5 cm.; calyx 7–9 mm. long, equally 5-parted to about the middle, the segments lanceolate; corolla 18–25 mm. long, somewhat purplish, especially on upper lip, the lip 4–6 mm. long,

with oblong-ovate lobes, these somewhat carinate and narrowed abruptly into short recurved teeth; lower lip without well developed palatal folds, truncate at base of lobes; anthers glabrous; stigma bilobed; capsule about as long as calyx.

KEY TO VARIETIES

Plants slender, the stems 2–4 dm. long, puberulent, with bracts ca. 5 mm. long; calyx 7 mm. long; corolla 20–25 mm. long. Lower California..... 1a. *O. multicaulis* var. *genuina*

Plants rather coarse, the stems 0.5–1.2 dm. long, pruinose, with bracts 6–10 mm. long; calyx 8–10 mm. long; corolla 18–22 mm. Mexican mainland..... 1b. *O. multicaulis* var. *Palmeri*

1a. **Orobanche multicaulis** T. S. Brandg. var. **genuina** n. nom. (Pl. 38, fig. 1)

O. multicaulis T. S. Brandg. l.c.

Stems slender, 2–4 dm. long,[2] puberulent; cauline bracts ca. 5 mm. long; calyx 7 mm. long; corolla 20–25 mm. long, the upper lip ca. 6 mm., the lower ca. 5 mm. long.

Type locality, Purissima, Lower California. Material seen, LOWER CALIFORNIA: Purissima, *Brandegee* in 1889, type (C); Calmalli, *Purpus 13* (C, S); Guadalupe, *T. S. Brandegee* in 1890 (C).

1b. **Orobanche multicaulis** var. **Palmeri** n. var. (Pl. 38, fig. 2)

Stems rather coarse, 5–12 cm. tall, pruinose; cauline bracts 6–10 mm. long; calyx 8–9 mm. long; corolla 18–22 mm. long, the upper lip ca. 5, the lower ca. 4 mm. long. (Caules crassi, 5–12 cm. alti, pruinosi; bracteis 6–10 mm. longis; calyce 8–9 mm. longo; corolla 18–22 mm. longa, labiis 4–5 mm. longis.)

Type, from city of Durango, Mexico, at 6207 ft. alt., on *Baccharis*, collected April, 1896, *Dr. E. Palmer 7* (Gray Herbarium). Isotype at California. Additional material, DURANGO: San Ramon, *Palmer 206* (C, G), *108* (G).—SAN LUIS POTOSI: Minas de San Rafael, *Purpus 5586* (C); Zapatillo, *Palmer 567* (G).—PUEBLA: Esperanza, *Purpus 3020* (C); Tehuacan, *Pringle 7022* (G).

These collections have passed as *O. Ludoviciana*, but constitute an entity quite different from that species in the bilobed stigma, lack of palatal folds, and in the cuspidate character of the corolla-lobes. In these respects it is quite like *O. multicaulis* of Lower California and is certainly not more than varietally distinct from Brandegee's plant.

2. **Orobanche Dugesii** (S. Wats.) n. comb. (Pl. 38, fig. 3)

Aphyllon Dugesii S. Wats. Proc. Am. Acad. **18**: 132. 1883.

Glabrate, coarse-stemmed, 5–15 cm. tall, simple and spicate, or with few spicate branches; cauline scales obtuse, 7–10 mm. long; flowers nearly or quite

[2] In giving height of plant, no attempt is made to distinguish between parts above and below ground.

sessile; calyx 7–8 mm. long, cleft to below the middle with lance-linear lobes; corolla apparently quite yellowish, thin, membranous, 15–17 mm. long, the lips ca. 3 mm. long with broad lobes which are scarcely toothed at the tips and quite truncate between the bases on the lower lip; anthers quite glabrous; stigma bilobed; capsule about as long as calyx.

Type locality, Guanajuato, Mexico. Material seen, Guanajuato, *Dugès* in 1880, type (G); in 1887 (G), in 1893 (G).

3. OROBANCHE BULBOSA G. Beck, Bibl. Bot. **4**: 73. 1890. (Pl. 38, fig. 4)

Phelipoea tuberosa Gray, Proc. Am. Acad. **7**: 371. 1867. *Aphyllon tuberosum* Gray, Bot. Calif. **1**: 585. 1876; Syn. Fl. **2**[1]: 313. 1878. *Orobanche tuberosa* (Gray) Heller, Cat. N. Am. Pl. 7. 1898. Not *Orobanche tuberosa* Hook. Fl. Bor. Am. **2**: 92. 1838, which is *Boschniakia tuberosa*. *Myzorrhiza tuberosa* (Gray) Rydb. Bull. Torrey Club **36**: 695. 1909.

Stout, dark, 1–3 dm. tall; pruinose-puberulent throughout, with thickened tuber-like base; cauline bracts lanceolate to acuminate, closely placed, ca. 1 cm. long; inflorescence densely pyramidal, thyrsoid-paniculate, the flowers nearly or quite sessile; calyx ca. 1 cm. long, somewhat exceeding the subtending bracts, unequally divided into lanceolate segments equaling or exceeding the tube; corolla ca. 12–15 mm. long, yellowish to purplish or brownish, the lips erect, 2.5–3.5 mm. long, usually with acute and sublanceolate lobes and lacking palatal folds in the throat; anthers white, glabrate, somewhat apiculate; stigma discoid; capsule almost as long as calyx.

Type locality, Gavilan Mts., Monterey County, California. Representative material, CALIFORNIA: Sweetwater, Eldorado Co., *K. Brandegee* in 1907 (C); Calaveras Co., *Davy 1625* (C); Miller Canyon, Solano Co., *Jepson* in 1897 (G, S); Mt. Diablo, Contra Costa Co., *Kellogg* (C), *Bioletti* in 1894 (C, P, S); Coal Mine Ridge, San Mateo Co., *Ferris* in 1917 (S); Loma Prieta, Santa Clara Co., *Hichborn* in 1920 (S); east of Madrone Springs, *Dudley* in 1895 (S); Tassajara Hot Springs, Monterey Co., *Elmer 3239* (S); Gavilan Mts., *Brewer 743*, type coll. (C, G); Santa Rosa Island, Santa Barbara Co., *T. S. Brandegee* in 1888 (C); Topatopa Mts., Ventura Co., *Abrams & McGregor 112* (S); Catalina Island, Los Angeles Co., *McClatchie* in 1893 (S); Glendora, *Grant 881* (C); Evey Canyon, San Antonio Mts., *Johnston 1430* (C, G, P, S); Cajon Pass, San Bernardino Co., *S. B. & W. F. Parish 1861* (C, G, S); San Bernardino, *Feudge 568* (P); head of City Creek Grade, *Munz 11310* (P); Idyllwild, Riverside Co., *Spencer 824a* (G); Murietta, *Munz & Johnston 5330* (C, P); Santa Ysabel, San Diego Co., *Munz 9814* (P); Pine Valley, *Spencer 1988* (P); near San Diego, *Orcutt 280* (C).

Parasitic on *Adenostoma* and associates in the chaparral belt of California, and for the most part quite consistent in its characters. *Williamson 72* from Rawhide Hill, Tuolumne Co. (P, S) differs from the other material I have seen in having rounded corolla-lobes.

4. OROBANCHE PINORUM Geyer, ex Hook. Kew Jour. **3**: 297. 1851. (Pl. 38, fig. 5)

O. pinorum in G. Beck, Bibl. Bot. **4**: 84. 1890. *Phelipoea pinetorum* Gray, Proc. Am. Acad. **7**: 371. 1867. *Aphyllon pinetorum* A. Gray, Bot. Calif. **1**: 585.

1876 and Syn. Fl. **2**[1]: 313. 1878. *Myzorrhiza pinorum* Rydb. Bull. Torrey Club **36**: 695. 1909.

Plant 1–3 dm. tall, glandular- and cinereous-pubescent, from a tuberous base, simple or with few erect branches in upper half; cauline scales lanceolate, acute to obtuse, 5–7 mm. long; pedicels 3–6 mm. long; calyx 6–8 mm. long, the lance-subulate lobes about half the total length; corolla 13–19 mm. long, yellowish, glandular-pubescent, the lips erect, 3–4 mm. long, the lobes acute, upper ones 1.5 mm., lower 3 mm. long; anthers glabrous; stigma disciform; capsule equaling and rupturing calyx.

Type locality, 'top of the high mts. near St. Joseph, Coeur d'Aleine country,' Idaho. Ranging from northern California to Washington and Idaho, parasitic on conifers. Material seen, IDAHO: Lamb Creek, *Epling & Houch 10238* (Univ. Calif. at Los Angeles); Gold Hill, *Howard & Ellison* in 1928 (UCLA).—WASHINGTON: Columbia Valley, bet. lat. 46° & 49° N., *Lyall* in 1860 (G); W. Klickitat Co., *Suksdorf 2782* (S).—OREGON: without locality, *E. Hall 364* (G).—CALIFORNIA: Pilot Creek, Humboldt Co., *Chestnut & Drew* in 1888 (C).

5. OROBANCHE GRAYANA G. Beck, Bibl. Bot. **4**: 79. 1890.

Orobanche comosa Hook. Fl. Bor. Am. **2**: 93. *pl. 169*. 1838. *Anoplanthus comosus* Walp. Rep. **3**: 480. 1844. *Phelipoea comosa* A. Gray, Pac. R. R. Rep. **4**: 118. 1857. *Aphyllon comosum* A. Gray, Bot. Calif. **1**: 584. 1876; Syn. Fl. **2**[1]: 312. 1878. Not *Orobanche comosa* Wallroth, Sched. Critic. **1**: 314. 1822. *Myzorrhiza Grayana* Rydb. Bull. Torrey Club **36**: 695. 1909.

Usually corymbose, sometimes paniculate, 5–35 cm. tall, glandular-puberulent throughout; pedicels well defined, 5–25 mm. long; calyx with filiform-subulate lobes; corolla strongly 2-lipped, the lips 7–15 mm. long, the upper reflexed, the lower spreading, with the palatal folds well developed; anthers woolly-pubescent; stigma peltate; seeds oblong-ovoid, favose-reticulate, ca. 0.3 mm. long.

KEY TO VARIETIES

Corolla 40–45 mm. long, lurid purple. Coastal, San Luis Obispo Co., to Mendocino Co., California.....5a. *O. Grayana* var. *violacea*

Corolla 25–35 mm. long, whitish to rose-purple or purplish brown.

Cauline bracts mostly ovate and obtuse; corolla purplish.

Plants slender, commonly 8–15 cm. tall; corolla tube slender, the lips purplish; calyx 14–16 mm. long. On *Grindelia*, etc. along coast from Monterey, California to British Columbia.....5b. *O. Grayana* var. *Nelsonii*

Plants coarse, 12–20 cm. tall; corolla tube rather broad, the lips purplish brown; calyx 8–15 mm. long. On *Artemisia tridentata;* mts. of S. California.....5c. *O. Grayana* var. *Feudgei*

Cauline bracts lanceolate to lance-linear, acute or acuminate; corolla whitish to pinkish, with darker veins.

Calyx 15–20 mm. long; plants 1–3 dm. tall. On *Baccharis, Grindelia*, etc. at low altitudes from southern to central California..5d. *O. Grayana* var. *Jepsonii*

Calyx 12–16 mm. long; plants 5–10 cm. tall. About meadows, on *Erigeron*, etc. from Tahoe, California to E. Washington.....5e. *O. Grayana* var. *typica*

5a. **Orobanche Grayana** var. **violacea** (Eastw.) n. comb. (Pl. 38, fig. 6)

Aphyllon violaceum Eastw. Zoe **5**: 85. 1900. *Orobanche comosa* var. *violacea* (Eastw.) Jeps. Man. Fl. Pl. Calif. 952. 1925.

Calyx 20–25 mm. long; corolla purple to dark violet, 40–45 mm. long; upper lip 12–18 mm. long, the lobes obtuse, lower lip 10–15 mm. long.

Type locality, Vision Hill, west of Tomales Bay, Marin Co., California. On *Grindelia*, along clay mesas and bluffs overlooking the sea, from San Luis Obispo County to Mendocino County. Representative material, CALIFORNIA: Cambria, San Luis Obispo Co., *Feudge 1771* (P); Farallone City, *Setchell 173* (C, G, P, S); Montara Point, *Copeland 3330* (P); Vision Hill, Marin Co., type coll., *Eastwood* in 1900 (C); Ft. Bragg, Mendocino Co., *Eastwood 1639* (G). Intergrading somewhat with plants like the var. *Nelsonii:* for example, a specimen from Pacific Grove, *Patterson & Wiltz* (S), with smaller flowers than var. *violacea*.

5b. **Orobanche Grayana** var. **Nelsonii** n. var. (Pl. 38, fig.7)

Corymbose, 8–15 cm. tall; cauline bracts mostly ovate and obtuse; calyx 8–16 mm. long; corolla purplish, 25–30 mm. long, the lips 7–10 mm. long. (Bracteae ovatae et obtusae; calyce 8–16 mm. longo; corolla purpurea, 25–30 mm. longa, labiis 7–10 mm. longis.)

Type, from low meadow, one mile north of Salem, Oregon, *J. C. Nelson 2479*, Oct 18, 1918 (Gray Herbarium). Coastal in distribution from central California to British Columbia, growing on *Grindelia*. Material seen, BRITISH COLUMBIA: Victoria, *Macoun 749* (G).—WASHINGTON: Shaw Island, *S. M. & E. B. Zeller 890* (G).—OREGON: Salem, *J. C. Nelson 2940* (G, S).—CALIFORNIA: Point Arena, Mendocino Co., *Davy & Blasdale 6039* (C); Seaside Station near Monterey, *K. Brandegee* in 1910 (C); Pacific Grove, *Coleman* in 1905 (S), *Dudley* in 1905 (S).

5c. **Orobanche Grayana** var. **Feudgei** n. var. (Pl. 38, fig. 8)

Plant 1–2 dm. tall; the cauline bracts ovate, obtuse, commonly about 5 mm. long; inflorescence capitate-corymbose; calyx 14–16 mm. long; corolla commonly purplish brown, with lower lip yellow at base, the upper lip 10–12 mm. long and almost as broad, its lobes 2.5–3 mm. long, the lower lip 9–10 mm. long. (Bracteae ovatae, obtusae, 5 mm. longae; calyce 14–16 mm. longo; corolla purpureo-brunnea, labiis 9–12 mm. longis).

Type, from dry rocky slope above Baldwin Lake, San Bernardino Mts., California, at 7500 feet altitude, *Munz 8177*, June 2, 1924, Pomona College Herbarium Number 48916. Montane at from three to eight thousand feet, apparently largely on *Artemisia tridentata*, in the mountains of southern California and adjacent Lower California. Named for Mr. J. B. Feudge of San Bernardino, California, whose discriminating collecting has added much to our knowledge of the California flora. Representative material, CALIFORNIA: Bisse's Station, Kern Co., *Dudley 393* (S); Lockwood Valley, Mt. Pinos region, Ventura Co., *Dudley & Lamb 4612* (P, S); Seymour Creek, *Munz 6974a* (P); Griffins, *Elmer 4159* (S); Pine Flats, Los Angeles Co., *Peirson 1178* (FP);

Swartout Valley, *Peirson* in 1922 (P); Big Pines, *Feudge 569* (P); ridge south of Swartout, *Munz 7687* (P); San Antonio Mt., San Bernardino Co., *Abrams 2675* (G, S); Holcomb Valley, *Munz 10645* (P); Baldwin Lake, *Munz 8177* (P); San Jacinto Mts., Riverside Co., *Hall 2135* (C, S); Santa Rosa Mts., *Munz 5827* (C, P); Ansa, *Munz 10897* (P); Palomar Mt., San Diego Co., *Munz 10388* (P); Jacumba, *Mearns 3339* (G, S).—LOWER CALIFORNIA: Hanson's Ranch, *Orcutt 896* (C, G).

5d. **Orobanche Grayana** var. **Jepsonii** n. var. (Pl. 38, fig. 10)

Corymbose, 1–3 dm. tall; cauline bracts lanceolate to lance-linear, 8–12 mm. long; calyx 15–20 mm. long; corolla mostly pinkish, 28–35 mm. long, the lips 10–12 mm. long. (Bracteae lanceolatae, 8–12 mm. longae; calyce 15–20 mm. longo; corolla rosea, 28–35 mm. longa, labiis 10–12 mm. longis.)

Type, Princeton, Colusa Co., California, *H. P. Chandler*, Oct., 1905, on *Baccharis*, Pomona College Herbarium No. 15,866; isotype at Stanford. Growing on *Baccharis*, *Grindelia*, etc., at low altitudes, mostly away from the coast and in central California. Material seen, CALIFORNIA: Duncan Mills, Sonoma Co., *Jones* in 1882 (P); Colusa Co., Colusa-Williams road, *Stinchfield 451* (S); Sycamore Slough, *Stinchfield 475* (S); Puerta Canyon, Stanislaus Co., *Brewer 1260* (C, G); Mt. Oso, *Brewer 1273* (C, G); Santa Cruz, *Jones 242* (P); San Joaquin Bridge, *T. S. Brandegee* in 1901 (C); Pinegrove, Amador Co., *Hansen 247* (C, P, S); Visalia, Tulare Co., *Congdon* in 1881 (S).

Most of the plants here referred to this variety were included in *O. comosa* var. *vallicola* Jepson, Man. Fl. Pl. Calif. 952. 1925. The type collection of that variety, however, *Jepson 6196* from Coyote, Santa Clara County is, to my way of thinking, to be referred to *O. californica* var. *typica*, hence the name *Jepsonii* for this concept, characterized by the long slender calyx-segments, light-colored corolla, and rather large size of the plants, namely 1–3 dm.

5e. **Orobanche Grayana** var. **typica** n. nom. (Pl. 38, fig. 9)

O. Grayana G. Beck, l.c. *O. comosa* Hook. Fl. Bor. Am. **2**: 93. *pl. 169*. 1838.

Low, 5–10 cm. tall, usually rather few flowered; cauline bracts lanceolate, 5–10 (12) mm. long; calyx 12–16 mm. long, the lobes lance-linear; corolla 25–30 mm. long, very pale with darker veins, the lips 10–14 mm. long.

Type locality, 'Banks of the Columbia,' collected by Douglas. Ranging from eastern Washington south to Lake Tahoe. Of the plants cited below, *Brandegee 1030* and *Mackay 3* have emarginate corolla-lobes as figured by Hooker. The other specimens have the lobes acute, but the difference is so slight as to seem unworthy of nomenclatural separation. Material seen, WASHINGTON: Soap Lake, Grand Coulee, *Mackay 3* (G); Oroville, *Jones* in 1911 (P); Washington territory, without locality, *Cooper* in 1853 (G); Walla Walla region, *T. S. Brandegee 1030* (G); Falcon Valley, Klickitat Co., *Suksdorf* in 1882 (C, G).—CALIFORNIA: Brockway, Placer Co., *Hall & Chandler 4551* (C); Tahoe Tavern, *Beans* in 1914 (G).

6. OROBANCHE CALIFORNICA C. & S. Linnaea **3**: 134. 1829.

Phelipoea californica G. Don, Gen. Syst. **4**: 632. 1838. *Aphyllon californicum* Gray, Bot. Calif. **1**: 584. 1876; Syn. Fl. **2**^{1}: 312. 1878. *Myzorrhiza californica* (C. & S.) Rydb. Bull. Torrey Club **36**: 695. 1909.

Usually spicate to paniculate, 5–30 cm. tall, glandular-pubescent; pedicels 2–15 mm. long; calyx-segments narrow and acuminate; corolla 2-lipped, the lips 2–8 mm. long, the upper erect, the lower slightly spreading and with 2 palatal folds from base into throat; anthers glabrate except in var. *corymbosa*, apiculate; stigma, capsules and seeds as in preceding species.

KEY TO VARIETIES

Upper lip of corolla divided almost to base, its lobes and those of lower lip about 8 mm. long, acute; plants corymbosely paniculate, 1–2 dm. tall. Los Angeles Co., California ..... 6a. *O. californica* var. *claremontensis*

Upper lip of corolla divided only part way.

Corolla purplish on upper lip at least; anthers quite woolly; plant low, 5–12 cm. tall, subcorymbose. Washington to California east of the Sierra Nevada, to Utah... 6b. *O. californica* var. *corymbosa*

Corolla pale in color, yellowish with darker veins; anthers glabrate.

Corolla ca. 25 mm. long; plants 1–3 dm. tall, with very numerous crowded flowers. Central California ..... 6c. *O. californica* var. *typica*

Corolla 18–22 mm. long; plants 0.5–1.5 dm. tall, with fewer, more scattered flowers. Mts. of southern California ..... 6d. *O. californica* var. *Parishii*

6a. **Orobanche californica** var. **claremontensis** n. var. (Pl. 39, fig.11)

Corymbosely paniculate, 1–2 dm. tall, many flowered; stems with few bracts, the lower ones suborbicular; calyx ca. 1 cm. long, the segments lance-linear; corolla ca. 25 mm. long, light in color, with pale purplish tinge, especially in upper lip, the lips ca. 8 mm. long, lobed to base, acute; anthers glabrate. (Plantae corymbose paniculatae; lobis corollae pallidis, ca. 8 mm. longis, acutis).

Type, from Claremont, Los Angeles Co., California, *D. L. Crawford 547*, July 8, 1916, Pomona College Herbarium No. 4356; isotypes at California, Gray, and Stanford.

Apparently on *Quercus agrifolia*. Other material, Claremont, *Harwood 3275* (P). Quite intermediate between *O. Grayana* and *O. californica*, resembling the former in the length of the corolla-lobes and the latter in the glabrous anthers and erect position of the lips of the corolla.

6b. **Orobanche californica** var. **corymbosa** (Rydb.) n. comb. (Pl. 39. fig. 12)

Myzorrhiza corymbosa Rydb. Bull. Torrey Club **36**: 696. 1909.

Plant low, 5–12 cm. tall, light colored, rather simple, subcorymbose; cauline bracts lance-ovate, 8–10 mm. long; calyx 12–18 mm. long, light in color; corolla 24–28 mm. long, the upper lip purple, ca. 5 mm. long, lower lip light or purplish, ca. 4 mm. long; anthers rather hairy.

Type locality, Reynold's Creek, Idaho. Growing apparently on *Artemisia tridentata*, from eastern Washington and Californica to Wyoming and Utah. Representa-

tive material, WASHINGTON: Rock Island, Kittitas Co., *Sandberg & Leiberg 456* (C, G); Chelan, Okanogan Co., *Elmer 506* (P).—OREGON: Union, *Cusick 126* (G); Squaw Creek, Malheur Co., *Cusick 2669* (C, G, P).—IDAHO: Nampa, Canyon Co., *Nelson & Macbride 1082* (G, S).—WYOMING: Jackson's Hole, *Merrill & Wilcox 1177* (G).—UTAH: Lake Point, Tooele Co., *Jones 1847* (S); Stansbury Island, *Leonard* in 1883 (G); Fish Lake, Sevier Co., *Jones 57* (P); 50 miles north of St. George, *Palmer 390* (G).—NEVADA: Unionville, Pershing Co., *Watson 763* (G); between Austin and Big Creek, Lander Co., *Kennedy 4515* (S); Reno, *Jones* in 1900 (P); Charleston Mts., *Jaeger* in 1926 (P).—CALIFORNIA: Tahoe, Placer Co., *Sonne 283* (C, S); Independence, Inyo Co., *Hall & Chandler 7221* (C); Cottonwood Creek, Tulare Co., *Copeland* in 1899 (S).

6c. **Orobanche californica** var. **typica** n. nom. (Pl. 39, fig. 13)

O. californica C. & S. Linnaea **3**: 134. 1829. *O. comosa* var. *vallicola* Jepson, Man. Fl. Pl. Calif. 952. 1925.

Plant 1–3 dm. tall, spicate or paniculate; lower pedicels usually not over 1–2 cm. long; cauline bracts remote, lanceolate to ovate, 8–12 mm. long; flowers crowded, numerous; calyx 1–2 cm. long; corolla pale, with darker veins, 25 mm. long, upper lip ca. 8 mm. long, its lobes 2.5–3 mm. long, the lower lip 6–8 mm. long, with acute lobes; anthers glabrate.

Type locality, San Francisco. Growing in central California. Representative material: Anderson, Shasta Co., *Rich* in 1921 (S); Snow Mt., Lake Co., *Purpus 1215* (C); Mt. Diablo, Contra Costa Co., *Elmer 4958* (C, S); Saratoga, Santa Clara Co., *Jepson 5157* (G), *Fablinger* in 1894 (C); Coyote, *Jepson 6196*, type coll. *O. comosa* var. *vallicola* (G); Santa Lucia Mts., Monterey Co., *Palmer 338* (G).

I have not seen type material, but the coastal plants of central California answer so well the description of *O. californica* that there seems to be no doubt as to their status.

6d. OROBANCHE CALIFORNICA var. PARISHII Jepson, Man. Fl. Pl. Calif. 952. 1925. (Pl. 39, fig. 14)

Spicate or weakly paniculate, 5–15 cm. tall, several to many flowered; cauline bracts ovate, 5–8 mm. long, many nerved; calyx ca. 10 mm. long; corolla 18–22 mm. long, yellowish with darker veins, the lips 5–7 mm. long; stamens glabrate.

Type locality, Bear Valley, San Bernardino Mts., California. In the mountains of southern California, at elevations above 2500 ft. on *Eriodictyon*, *Hazardia*, etc. Material seen, CALIFORNIA: Ft. Tejon, Kern Co., *Hall 6301* (C); Cameron, *Jones* in 1900 (P); Evey Canyon, San Antonio Mts., *Johnston 1431* (P, S), *1429* (C); Devils Backbone, Mt. San Antonio, *Johnston 1762* (P, S), *1763* (G); trail to San Sevaine Flats, San Antonio Mts., *Johnston* in 1925 (P); Glen Martin, San Bernardino Mts., *Feudge 661* (P); Witch Creek, San Diego Co., *Alderson* in 1894 (C); Ramona, *Brandegee* in 1894 (C), in 1896 (C); Julian, *Brandegee* in 1894 (C).

For this variety I have not seen type material, but the submembranous character of the bracts and calyx, and the many parallel nerves mentioned by Jepson characterize the plants I have here referred to var. *Parishii*.

7. OROBANCHE LUDOVICIANA Nutt. Gen. N. Am. **2**: 58. 1818.

Phelipoea Ludoviciana Walp. Rep. **3**: 461. 1844–45. *Aphyllon Ludovicianum* A. Gray, Bot. Calif. **1**: 585. 1876; Syn. Fl. **2**^{1}: 313. 1878. *Myzorrhiza Ludoviciana* Rydb. in Small, Fl. S. E. U. S. 1093. 1903.

Plant 1–3 dm. tall, puberulent, more or less viscid, simple or with few loose branches; lower flowers on pedicels up to 1.5 cm. long; calyx 5–12 mm. long, cleft, the segments somewhat unequal; corolla usually purplish, especially on the upper lip, 12–30 mm. long, the lobes pointed, not rounded, erect; anthers usually somewhat pubescent, at least after dehiscence; stigma discoid, crateriform, capsule equaling or slightly exceeding calyx.

KEY TO VARIETIES

Corolla-lobes lanceolate, tapering gradually to acute tip; corolla 15–28 mm. long.
Anthers pubescent; upper lip of corolla 5–8 mm. long; plant yellowish to brown.
Lips of corolla 6–8 mm. long; calyx 10–12 mm. long; cauline bracts acute. Plains and prairies east of Rocky Mts. . . . . 7a. *O. Ludoviciana* var. *genuina*
Lips of corolla 3–6 mm. long; calyx 5–8 mm. long; cauline bracts obtuse, rounded. Deserts from western Texas to California. . . . 7b. *O. Ludoviciana* var. *Cooperi*
Anthers glabrous; upper lip of corolla 3 mm. long; whole plant very dark. San Gabriel Mts., southern California. . . . . 7c. *O. Ludoviciana* var. *valida*
Corolla-lobes broader, narrowed abruptly at tip; corolla 20–30 mm. long. Deserts from El Paso, Texas to California. . . . . 7d. *O. Ludoviciana* var. *latiloba*

7a. OROBANCHE LUDOVICIANA var. GENUINA G. Beck, Bibl. Bot. **4**: 81. 1890. (Pl. 39, fig. 15)

O. Ludoviciana Nutt. Gen. N. Am. **2**: 58. 1818.

Stout, viscid-puberulent, 1–2 dm. tall, spicate; cauline bracts 5–10 mm. long, lanceolate to lance-ovate; lower flowers on pedicels up to 1 cm. long; cauline bracts lance-linear, ca. 1 cm. long; calyx 10–12 mm. long, the lobes lance-linear, somewhat unequal; corolla purplish, especially on upper lip, 15–20 mm. long, the lips erect, 6–8 mm. long, the lobes acute, almost lanceolate; anthers somewhat pubescent, at least after dehiscence.

Type locality, Ft. Mandan, North Dakota. Growing on *Grindelia*, *Ambrosia*, etc. in the plains region east of the Rocky Mountains. Material seen, SASKATCHEWAN: Plains, *Macoun 1228* (G).—MONTANA: Otter Creek, *Anderson 54* (C).—COLORADO: Golden, *Greene* in 1870 (G).—ILLINOIS: Dixon, *Vasey* (G); Athens, Menard Co., *E. Hall* in 1861 (G, P); White Co., collector not named, in 1909 (G).—NEBRASKA: Deuel Co., *Rydberg 5* (G); Minden, *Hapeman* in 1926 (S).—KANSAS: Stockton, *Bates* in 1908 (G).—TEXAS: Rio Brazos, *Drummond* (G); Uvalde, *Palmer 2025* (G).

7b. OROBANCHE LUDOVICIANA var. COOPERI (A. Gray) G. Beck, Bibl. Bot. **4**: 81. 1890. (Pl. 39, fig. 17)

Aphyllon Cooperi A. Gray, Proc. Am. Acad. **20**: 307. 1885; Syn. Fl. **2**^{1}: suppl. 455. 1886. *A. Ludovicianum* var. *Cooperi* Gray as synonym, in Proc. Am. Acad. *l.c. Orobanche Cooperi* Heller, Cat. N. Am. Pl. 7. 1898. *Myzorrhiza Cooperi* (A. Gray) Rydb. Bull. Torrey Club **36**: 695. 1909.

Stems rather slender, 1–3 dm. tall, somewhat enlarged at base, puberulent, usually somewhat branched; cauline scales 5–10 mm. long, obtuse; pedicels up to 15 mm. long; calyx 5–8 mm. long; corolla 15–28 mm. long, the lobes purplish, acute, the lips 3–6 mm. long; anthers somewhat pubescent after dehiscence.

Type locality, Ft. Mojave, Arizona. Largely on *Franseria dumosa*, on the deserts from California and Nevada to New Mexico and Sonora. There seem to be included here two series, one with rather large flowers, the true var. *Cooperi*, such as the *Pringle* collection from the Santa Catalina Mts. Arizona, having corollas 24 mm. long; the other series with corollas 15–20 mm. long, as *Munz, Johnston, & Harwood 4106*. The two intergrade so completely that I am unable to maintain any distinction between them. As representative of the variety *Cooperi* may be cited, TEXAS: El Paso, *Vasey* in 1878 (C).—NEW MEXICO: Socorro, *Snow 6417* (S).—NEVADA: Mesquite Well, *Goodding 2248* (G).—SONORA: Pinacate, *Lumholtz 5* (G); Lerdo, *Palmer 937* (G).—ARIZONA: Lowell, *W. F. Parish 190* (G, S); Santa Catalina Mts., *Pringle* in 1884 (G); Hackberry, *Jones* in 1884 (P); Yucca, *Jones* in 1884 (P); Ft. Mojave, *Cooper* in 1860, type (G).—CALIFORNIA: Darwin Mesa, *Hall & Chandler 7169* (C); Ord Mt., *Jepson 5893* (G); Ludlow, *Munz & Harwood 3410* (P); Hector, *Munz, Johnston, & Harwood 4106* (P); Palm Springs, *Spencer 1988* (G); Indio, *Jones* in 1906 (P); Salton, *Jaeger 1056* (P); foot of Mt. Springs Grade, *Peirson 4064* (FP); Chuckwalla Springs, *Hall 5894* (C).

It seems quite conservative to reduce this desert inhabitant to a variety of *O. Ludoviciana*, but the characters distinguishing it are very slight.

7c. **Orobanche Ludoviciana** var. **valida** (Jepson) n. comb. (Pl. 39, fig. 16)

O. valida Jepson, Madrona **1**: 255. 1930.

Whole plant dark, of brownish purple color, spicate, 1–2 dm. tall, rather slender, simple or with few branches; cauline bracts lanceolate, ca. 1 cm. long; pedicels short, the lowest barely 1 cm. long; calyx 7–9 mm. long, the segments lance-acuminate; corolla 12–14 mm. long, brownish purple, upper lip 3–4 mm. long, purple, the 2 lobes acute; lower lip 3 mm. long, yellowish, each lobe with dark purple midvein; anthers glabrous.

Type locality, Rock Creek, San Gabriel Mts., Los Angeles Co., Calif. Material seen, CALIFORNIA, San Gabriel Mts., south trail to 'Baldy Lookout,' *Johnston 5290* (P); south fork Rock Creek, *Mabel Peirson* in 1928, type coll. (FP).

7d. **Orobanche Ludoviciana** var. **latiloba** n. var. (Pl. 39, fig. 18)

Stem coarse, 1.5–3 dm. tall, puberulent, usually somewhat loosely branched; cauline bracts 5–8 mm. long, broad, suborbicular; calyx 10 to 12 mm. long; corolla 20–30 mm. long, purplish especially on upper lip, the lips erect, 6–9 mm. long, the lobes broad, abruptly narrowed at tip; anthers somewhat hairy. (Corolla 20–30 mm. longa, lobis latis, abrupte angustatis apice.)

Type, on roots of *Hymenoclea Salsola*, in sandy wash at south base of Eagle Mts., Colorado Desert, Riverside County, California, *Munz & Keck 4960*, April 13, 1922, Pomona College Herbarium No. 14178; isotype at Stanford.

With much the same distribution as var. *Cooperi*, on the deserts of the Southwest, and confused with that variety, but with a very differently proportioned corolla. Representative material, CALIFORNIA: 12 miles east of Palmdale, L. A. Co., *Peirson 6728* (FP); Victor, *Wright* in 1888 (C); Fishponds, Mojave Desert, *Parish* in 1883 (S); Funeral Mts., *Coville & Funston 434* (G, S); Dos Palmos, Colorado Desert, *Munz 9977* (P); Travertine Rock, *Jaeger* in 1918 (S).—S. UTAH: *Parry 145* (G), apparently this.—NEW MEXICO: without locality, *C. Wright 1449*, in 1851 (G), *1450* (G), *426*, in 1849 (G). Near El Paso, *Wright 1261*, in 1849 (G).

8. OROBANCHE MULTIFLORA Nutt. Jour. Acad. Nat. Sci. Phila. II. **1**: 179. 1848.

Aphyllon multiflorum (Nutt.) A. Gray, Bot. Calif. **1**: 585. 1876; Syn. Fl. **2**[1]: 313. 1878. *Orobanche Ludoviciana* Nutt. var. *multiflora* (Nutt.) G. Beck, Bibl. Bot. **4**: 81. 1890. *Myzorrhiza multiflora* (Nutt.) Rydb. Bull. Torrey Club **33**: 151. 1906.

Spicate to thyrsoid, 5–20 cm. tall, quite viscidly grayish pubescent throughout; flowers nearly sessile; cauline bracts lance-ovate to ovate, obtuse, 5–12 mm. long; calyx 8–17 mm. long, deeply 5-cleft into lance-linear lobes; corolla yellow, purplish, or reddish, especially on the limb, 15–35 mm. long, the lips rather erect, 5–12 mm. long, with lobes rounded at apex; anthers tufted with long hairs or almost glabrate; stigma crateriform; capsule equal to or about two-thirds the length of the calyx.

KEY TO VARIETIES

Corolla 25–35 mm. long, the upper lip 9–12 mm. long; anthers with numerous long hairs. Mts. of S. Colorado, New Mexico and adjacent Mexico..... 8a. *O. multiflora* var. *typica*

Corolla 15–25 mm. long, the upper lip 5–7 mm. long; anthers sparingly, if at all pubescent.

Anthers not conspicuously exserted, 2 mm. long; corolla purplish.

Lower lip of corolla 6–7 mm. long, upper lip ca. 7 mm. long, slightly broader, rosy or purplish. Chihuahua..... 8b. *O. multiflora* var. *Pringlei*

Lower lip of corolla 4 mm. long, upper 5 mm., purplish, slightly narrower. Colorado and Utah to Montana and Washington..... 8c. *O. multiflora* var. *arenosa*

Anthers conspicuously exserted, 3 mm. long; corolla yellow. New Mexico..... 8d. *O. multiflora* var. *xanthochroa*

8a. **Orobanche multiflora** var. **typica** n. nom. (Pl. 39, fig. 19)

O. multiflora Nutt. *l.c.* *Phelipoea erianthera* Engelm. in A. Gray, Proc. Am. Acad. **7**: 372. 1867.

Plant 10–20 cm. tall, pruinose-puberulent; cauline bracts ovate, obtuse, 5–12 mm. long; calyx 12–17 mm. long; corolla 25–35 mm. long, with purplish limb, the upper lip 9–12 mm. long; anthers tufted with long hairs.

Type locality, 'Sandy ground along the borders of the Rio del Norte,' (Rio Grande). From New Mexico and adjacent Texas and Mexico. Characterized chiefly by the large size of the corollas and the copious long hair on the anthers. Material seen, NEW

MEXICO: Rayado Creek, Colfax Co., *Fendler 585* (G); Albuquerque, *Jones* in 1904 (P). —COLORADO: Huerfano Valley, *Parry 147*, type coll. *P. erianthera* (G).—TEXAS?: Ft. Smith to the Rio Grande, *Bigelow* in 1853–4 (G); El Paso, *Vasey* in 1878 (C).—MEXICO: Saltillo, *Palmer 995* (G); Monterey, *Canby 183* (G); Chihuahua, *Thurber 1049* (G).

8b. **Orobanche multiflora** var. **Pringlei** n. var. (Pl. 39, fig. 20)

Plant 10–15 cm. tall; cauline bracts ovate, obtuse, 5–12 mm. long; calyx 8–10 mm. long, the segments lanceolate; corolla 20–25 mm. long, the lips apparently rose-purple or paler, 5–7 mm. long; anthers sparingly pubescent. (Corolla 15–20 mm. longa; labiis 6–7 mm. longis, roseopurpureis, latis).

Type from near Chihuahua, Chihuahua, June 3, 1885, *Pringle 31* (G). Other material seen, CHIHUAHUA: *Pringle 78* (G).

8c. **Orobanche multiflora** var. **arenosa** (Suksdf.) n. comb. (Pl. 39, fig. 21)

Aphyllon arenosum Suksdf. Allg. Bot Zeitschr. **17**: 27. 1906.

Plant 5–15 cm. tall, fairly slender; cauline bracts lance-ovate; calyx 9–12 mm. long; corolla purplish on the limb, 15–20 mm. long, the upper lip ca. 5 mm. long; anthers quite glabrous.

Type locality, Bingen, Klickitat Co., Washington. On *Chrysopsis, Artemis,a,i* etc. ranging from eastern Washington to western Colorado, and California. Material seen, WASHINGTON: W. Klickitat Co., *Suksdorf 2248* (C, G); Bingen, *Suksdorf 2781*, type collection (C, G); Rock Island, Kittitas Co., *Sandberg & Leiberg 436* (C, G); WaWawai, *Piper 2842* (G, P).—WYOMING: Upper Geyser Basin, Yellowstone Park, *Setchell* in 1905 (C); Gardiner River, Yellowstone Park, *A. & E. Nelson 5994* (G); Glen Rock, *Evermann* in 1893 (S).—COLORADO: Naturita, *Payson 485* (G); Paradox, *Walker 190* (G).—CALIFORNIA: Providence Mts. San Bernardino Co., *Munz, Johnston, & Harwood 4049* (P). Material from Utah is confusing, as it intergrades with var. *typica;* the following collections have flowers ca. 20 mm. long, as in var. *arenosa*, but considerable hair on the anthers as in var. *typica:* Cottrell's Ranch, *Jones 5658* (P); Willow Springs Pass, *Jones* in 1891 (P); Lake Point, *Jones 1847* (P, S). *Jones 5794* (P) from Fish Lake is nearer var. *typica*.

8d. **Orobanche multiflora** var. **xanthochroa** (Nels. & Ckll.) n. comb.

O. xanthochroa Nels. & Ckll. Bot. Gaz. **37**: 278. 1904.

Corolla 16–18 mm. long, pale yellow, with rounded lobes; upper lip 6 mm. long, lower 3–4 mm. long; anthers 3 mm. long, exserted.

Type locality, Pecos, San Miguel Co., New Mexico. Type, collected in 1903 by Grabham (label says Cockerell), the only specimen seen. It is in the herbarium of the University of Wyoming.

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Explanation of plates 38, 39

Drawings made with the aid of camera lucida; they show in each case the limb of the dissected corolla, the upper lip being 2-lobed, the lower 3-lobed. Size of each corolla indicated below.

PLATE 38

Fig. 1. *Orobanche multicaulis* var. *genuina*, from type. Corolla 24 mm. long, the upper lip 6 mm. long.

Fig. 2. *O. multicaulis* var. *Palmeri*, from *Pringle 7022* (G). Corolla 19 mm. long, the upper lip 5 mm.

Fig. 3. *O. Dugesii*, from type. Corolla 17 mm. long, upper lip 3 mm.

Fig. 4. *O. bulbosa*, from *Feudge 568*. Corolla 12 mm. long, upper lip 4 mm.

Fig. 5. *O. pinorum*, from *Hall 364*. Corolla 19 mm. long, upper lip 3mm.

Fig. 6. *O. Grayana* var. *violacea*, from *Copeland 3330*. Corolla 40 mm. long, the upper lip 11 mm.

Fig. 7. *O. Grayana* var. *Nelsonii*, from *Macoun 749*. Corolla 32 mm. long, the upper lip 11 mm.

Fig. 8. *O. Grayana* var. *Feudgei*, from *Munz 7687*. Corolla 32 mm. long, the upper lip 10 mm.

Fig. 9. *O. Grayana* var. *typica*, from *MacKay 3*. Corolla 30 mm. long, the upper lip 10 mm.

Fig. 10. *O. Grayana* var. *Jepsonii*, from *Jones* collection at Duncan Mills. Corolla 30 mm. long, the upper lip 12 mm.

PLATE 39

Fig. 11. *Orobanche californica* var. *claremontensis*, from type. Corolla 26 mm. long, upper lip 8 mm.

Fig. 12. *O. californica* var. *corymbosa*, from *Cusick 2669*. Corolla 28 mm. long, upper lip 5 mm.

Fig. 13. *O. californica* var. *typica*, from *Jepson 6196*. Corolla 27 mm. long, upper lip 8 mm.

Fig. 14. *O. californica* var. *Parishii*, from *Johnston 1431*. Corolla 20 mm. long, upper lip 6 mm.

Fig. 15. *O. Ludoviciana* var. *genuina*, from the White Co., Ill. specimen at Gray Herbarium. Corolla 20 mm. long, the upper lip 8 mm.

Fig. 16. *O. Ludoviciana* var. *valida*, from *Johnston 5290*. Corolla 15 mm. long, the upper lip 3 mm.

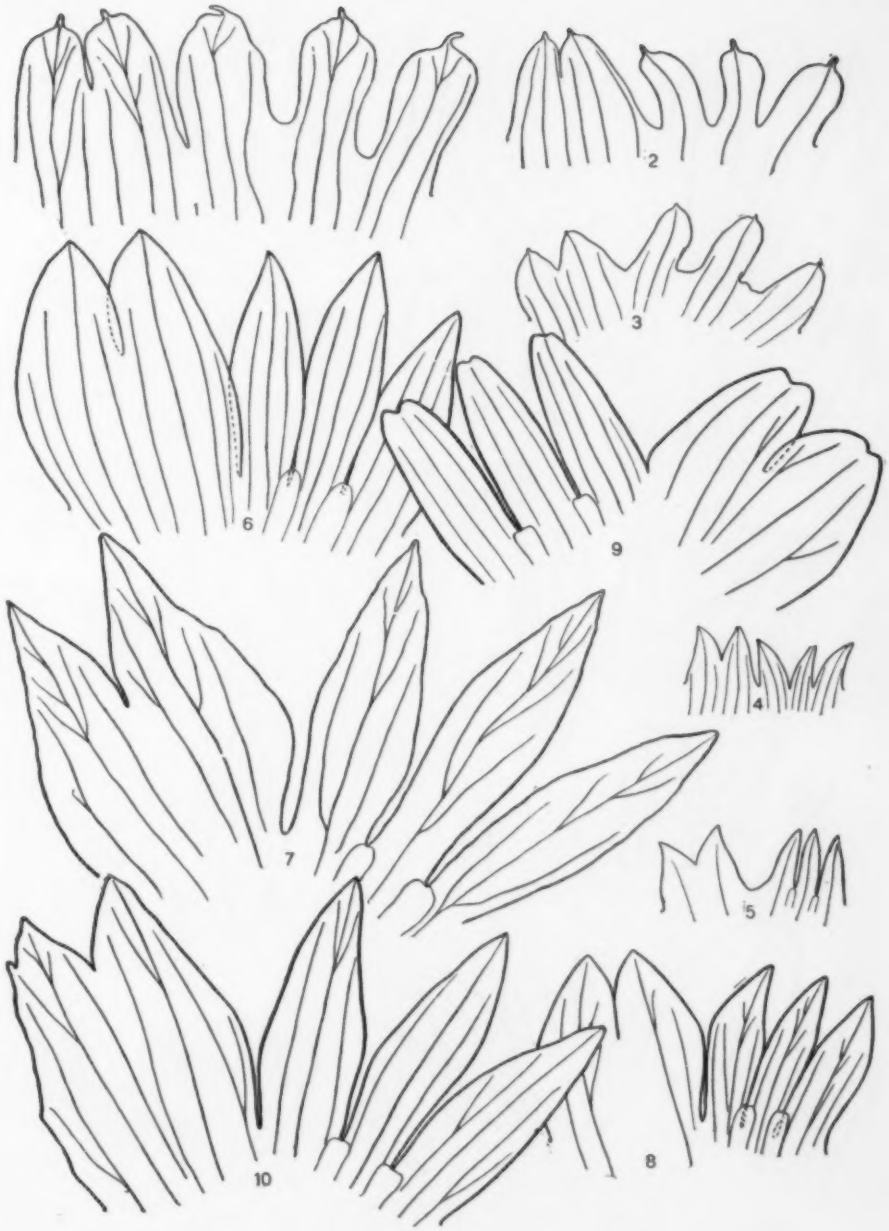
Fig. 17 *O Ludoviciana* var *Cooperi*, from the *Pringle* specimen from Santa Catalina Mts. Corolla 24 mm. long, the upper lip 6 mm.

Fig. 18. *O. Ludoviciana* var. *latiloba*, from type. Corolla 30 mm. long, the upper lip 10 mm.

Fig. 19. *O. multiflora* var. *typica*, from *Jones* collection made at Albuquerque. Corolla 35 mm. long, the upper lip 12 mm.

Fig. 20. *O. multiflora* var. *Pringlei*, from type. Corolla 24 mm. long, the upper lip 7 mm.

Fig. 21. *O. multiflora* var. *arenosa*, from isotype at Gray. Corolla 16 mm. long, the upper lip 5 mm.



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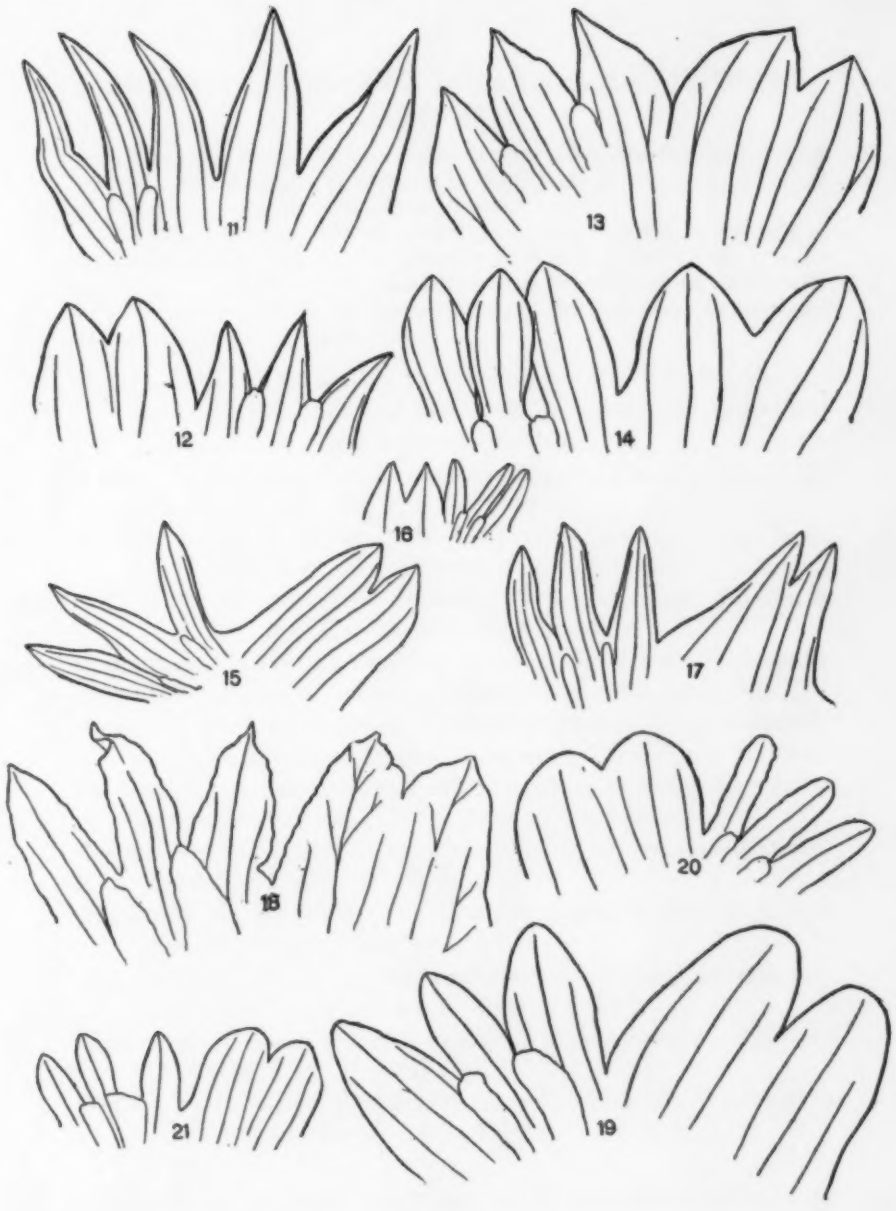

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INDEX TO AMERICAN BOTANICAL LITERATURE

1927–1931

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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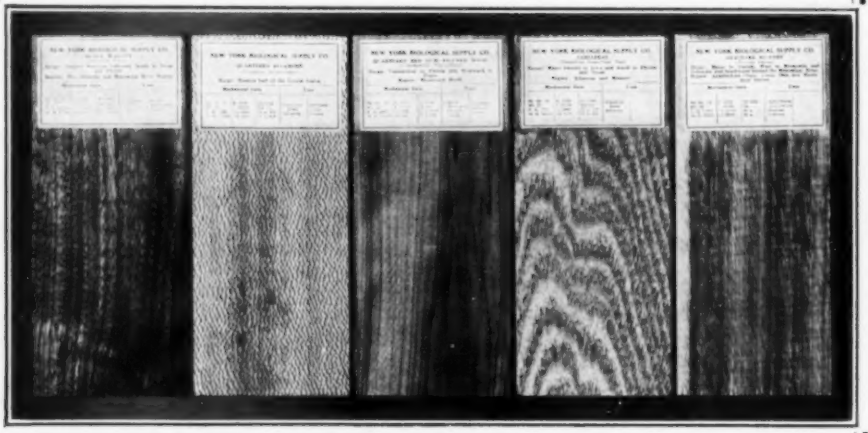

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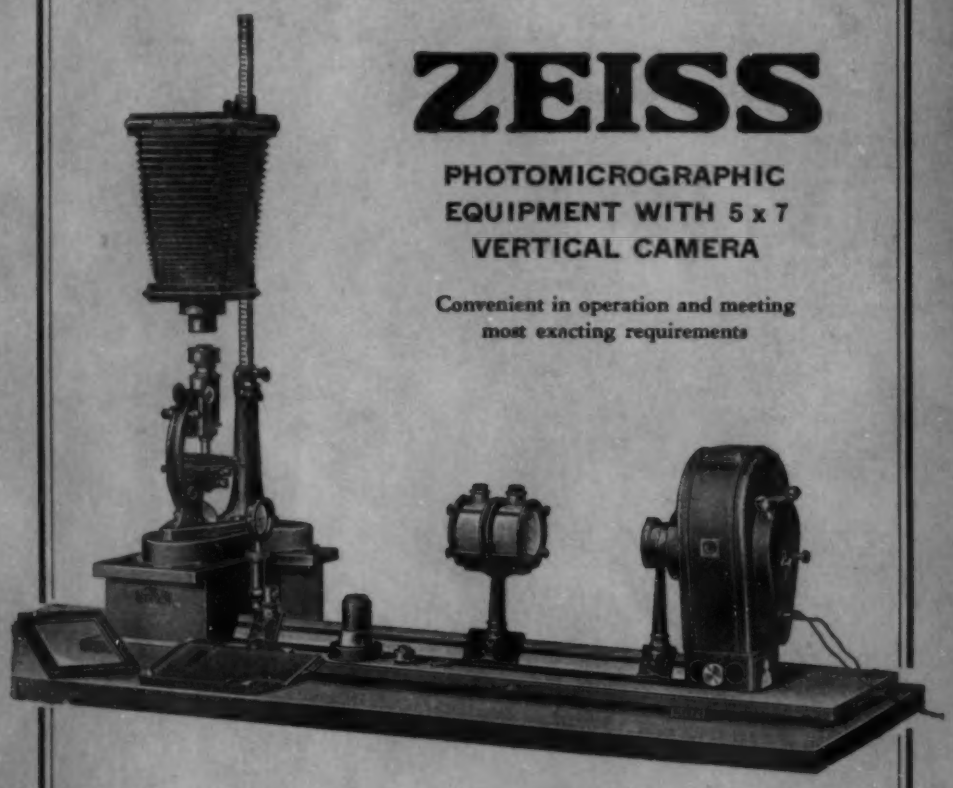

I. A. OUTFIT FOR TRANSPARENT OBJECTS with 400 Watt Incandescent Lamp. Camera with one double plate holder, sleeve for connection with microscope, table top with optical bench, plane 45° mirror, filter trough holder on rider with 2 troughs, centering lens holder on rider, centering lens Z 70/6, Lamp housing, one 400 Watt bulb 110 V., adjustable resistance for 110 V., collector 12.5 (6) cm with iris on rider. Price $238.75

B. ACCESSORIES FOR LOW MAGNIFICATIONS (as obtained with micro-planara, etc.)
Revolver with accessory collectors 100, 66, 33 for attachment to rider of collector 12.5 (6) cm (cannot be added later); Centering lens Z 40/6, Condenser K20 on rider, Iris diaphragm on rider. Price $47.00

C. ADDITIONAL RECOMMENDED ACCESSORIES:

2 extra 5 x 7 double plate holders @ $15.00	$30.00
Aplanatic Focusing magnifier 6x with locknut	10.00
6 kits for 3¼ x 4¼" plates @ 75c	4.50

II. FOR USE WITH VERTICAL ILLUMINATORS (for opaque objects) add:
Collector 14 (3.5) cm with iris on inclinable rider 13.00

Additional cost for a clock-feed arc lamp instead of incandescent lamp $48.00 for 110 V. d. c. or $56.50 for a. c. circuit.

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